UNIVERZA V LJUBLJANI
BIOTEHNIŠKA FAKULTETA

Matija KLOPČIČ

SESTOJNA DINAMIKA JELOVO-BUKOVIH GOZDOV V SLOVENIJI OD ZAČETKA NAČRTNEGA GOSPODARJENJA DO DANES

DOKTORSKA DISERTACIJA

FOREST STAND DYNAMICS OF SILVER FIR-EUROPEAN BEECH FORESTS IN SLOVENIA FROM THE BEGINNING OF REGULAR FOREST MANAGEMENT UNTIL THE PRESENT

DOCTORAL DISSERTATION

Ljubljana, 2011

... nature has functional, historical, and evolutionary limits. Nature has a range of ways to be, but there is a limit to those ways, and therefore, human changes must be within those limits.

(Christensen et al., 1996)

Moji družini,
še posebej moji mnogo prekmalu
preminuli mami!

To my family,
but especially to my beloved mother,
who died before she should have!

Doktorska disertacija je zaključek podiplomskega študija bioloških in biotehniških znanosti s področja gozdarstva in obnovljivih gozdnih virov in je nastala na Katedri za obnovljive gozdne vire, v Skupini za urejanje gozdov in biometrijo Oddelka za gozdarstvo in obnovljive gozdne vire Biotehniške fakultete Univerze v Ljubljani.

Na podlagi statuta Univerze v Ljubljani, sklepu Senata Biotehniške fakultete in sklepu Komisije za doktorski študij (po pooblastilu 30. seje Senata Univerze v Ljubljani 20. 1. 2009) z dne 12. 11. 2009 (št. odločbe 5-1708/09 VJJ) je bil za mentorja imenovan prof. dr. Andrej Bončina.

Komisija za oceno in zagovor:

Predsednik: doc. dr. David HLADNIK, Univerza v Ljubljani, Biotehniška fakulteta, Oddelek za gozdarstvo in obnovljive gozdne vire

Član: prof. dr. Andrej BONČINA, Univerza v Ljubljani, Biotehniška fakulteta, Oddelek za gozdarstvo in obnovljive gozdne vire

Član: prof. dr. Marco MARCHETTI, Universita degli Studi del Molise, Dipartimento di Scienze e Technoogie per l'Ambiente e il Teritiorio

Datum zagovora: 4. 8. 2011

Naloga je rezultat lastnega raziskovalnega dela. Podpisani se strinjam z objavo svoje naloge v polnem tekstu na spletni strani Digitalne knjižnice Biotehniške fakultete. Izjavljam, da je naloga, ki sem jo oddal v elektronski obliki, identična tiskani verziji. Izjavljam, da so vsa vključena znanstvena dela identična objavljeni verziji.

Matija Klopčič

KLJUČNA DOKUMENTACIJSKA INFORMACIJA

ŠD	Dd
DK	GDK 22:902(497.4)(043.3)=111=163.6
KG	arhivski viri podatkov/sestojna zgradba/*Fagus sylvatica*/*Abies alba*/*Picea abies*/ gozdna inventura/vplivni dejavniki/gospodarjenje z gozdovi/gozdnogojitveni sistemi/ antropogene motnje/naravne motnje/veliki rastlinojedi
KK	
AV	KLOPČIČ, Matija, univ. dipl. inž. gozdarstva
SA	BONČINA, Andrej, prof. dr. (mentor)
KZ	SI-1000 Ljubljana, Večna pot 83
ZA	Univerza v Ljubljani, Biotehniška fakulteta, Oddelek za gozdarstvo in obnovljive gozdne vire
LI	2011
IN	SESTOJNA DINAMIKA JELOVO-BUKOVIH GOZDOV V SLOVENIJI OD ZAČETKA NAČRTNEGA GOSPODARJENJA DO DANES
TD	Doktorska disertacija
OP	VII, 105 str., 249 vir.
IJ	en
JI	sl/en

AI Dinamika pretežno raznomernih jelovo-bukovih gozdnih sestojev v zadnjem stoletju in njeni poglavitni vplivni dejavniki so bili proučevani v treh prostorsko dislociranih raziskovalnih objektih (Jelovica, Trnovo in Leskova dolina). S pomočjo arhivskih podatkov iz gozdnih inventur in pripadajočih gozdnogospodarskih kart je bila izdelana GIS podatkovna zbirka, v kateri je bil odsek osnovna prostorska enota. Spremembe v zgradbi gozdnih sestojev so bile ovrednotene z izbranimi sestojnimi parametri: lesno zalogo, debelinsko strukturo, diverziteto debelinske strukture, drevesno sestavo in vrastjo dreves. V zadnjem stoletju so se proučevani sestojni parametri značilno spreminjali. Med objekti so bile odkrite značilne razlike v sestojni dinamiki, vendar tudi nekatere podobnosti. V proučevanem obdobju je lesna zaloga gozdnih sestojev v vseh raziskovalnih objektih stalno naraščala. Spremembe debelinske strukture so nakazale dva različna razvoja sestojev: povečevanje sestojne gostote in količine tanjšega drevja (»pomlajevanje sestojev«) na Jelovici in Trnovem in znižanje sestojne gostote ob hkratnem povečevanju količine debelega drevja (»staranje sestojev«) v Leskovi dolini. Med objekti so bile ugotovljene opazne razlike v diverziteti debelinske strukture, vrasti dreves in drevesni sestavi. Na Trnovem in v Leskovi dolini sta jelka in bukev v proučevanem obdobju izmenjaje prevladovali v lesni zalogi. Med glavnimi drevesnimi vrstami so bile največje spremembe obilja in debelinske strukture opažene pri jelki, vendar so se te spremembe med objekti razlikovale. V proučevanem obdobju so na različen razvoj jelovo-bukovih gozdov v treh analiziranih območjih najpomembneje vplivale razlike v pretekli rabi gozdov, režimih abiotskih in biotskih naravnih motenj in rastiščnih razmerah. Na podlagi presoje vplivov posameznih dejavnikov so bili podani predlogi za prihodnje gospodarjenje z jelovo-bukovimi gozdovi ter nakazane možnosti raziskav v prihodnosti.

KEY WORDS DOCUMENTATION

DN Dd
DC FDC 22:902(497.4)(043.3)=111=163.6
CX archival data sources/forest stand structure and composition/*Fagus sylvatica*/*Abies alba*/*Picea abies*/forest inventory/influential factors/forest management/silvicultural systems/anthropogenic disturbances/natural disturbances/large ungulates
CC
AU KLOPČIČ, Matija
AA BONČINA, Andrej (supervisor)
PP SI-1000 Ljubljana, Večna pot 83
PB University of Ljubljana, Biotechnical Faculty, Department of Forestry and Renewable Forest Resources
PY 2011
TI FOREST STAND DYNAMICS IN SILVER FIR-EUROPEAN BEECH FORESTS IN SLOVENIA FROM THE BEGINNING OF REGULAR FOREST MANAGEMENT UNTIL THE PRESENT
DT Doctoral Dissertation
NO VII, 105 p., 249 ref.
LA en
AL sl/en
AB The dynamics of silver fir-European beech forest stands in the last century and its main influential factors were studied in three geographically dislocated study areas in Slovenia, Jelovica, Trnovo, and Leskova dolina. The GIS database was created on a (sub)compartment spatial level using archival forest inventory data and forest management maps for a particular forest inventory period. Changes in forest stands were evaluated with selected structural and compositional indicators: stand volume, dbh structure, tree size diversity, tree species composition, and recruitment rate. Over the century-long time period, all studied stand parameters showed noticeable dynamics. Significant differences, as well as some similarities, in forest stand dynamics were observed at a regional spatial scale. The stand volume has been continuously increasing during the observation period in all study areas. Changes in dbh structure indicated two different directions of stand dynamics: the increase in stand densities and quantity of small-diameter trees ("the regeneration" of stands) in Jelovica and Trnovo, and the increase in quantity of large-diameter trees combined with the reduction in the number of trees ("ageing" of stands) in Leskova dolina. Diverse dynamics between the study areas were observed also in tree size diversity, recruitment rate, and tree species composition. In Trnovo and Leskova dolina study areas, fluctuations in dominance between fir and beech were observed. Among the main tree species, fir underwent the most large-scale changes, which varied between the study areas. Differences in past forest management, regimes of abiotic and biotic natural disturbances, and site conditions seem to be the most important impact factors of diverse long-term dynamics of fir-beech forest stands in Slovenia. The influences of particular impact factors were discussed and some implications for forest management and suggestions for future research were proposed.

KAZALO VSEBINE

OKRAJŠAVE IN SIMBOLI

DEM	digital elevation model; digitalni model reliefa
DI	disturbance index; indeks jakosti naravnih motenj
FC	full callipering; polna premerba
FMP	forest management plan; gozdnogospodarski načrt
FMU	forest management unit; gozdnogospodarska enota
GC	Gini coefficient; Ginijev koeficient
GIS	geographic information system; geografski informacijski sistem
KW	Kruskal-Wallis statistical test; Kruskal-Wallisov statistični test
OA	ocular assessment of stand parameters; okularna ocena sestojnih parametrov
PSP	permanent sampling plot; stalna vzorčna ploskev
RRI	recruitment rate index; indeks stopnje vrasti
SVI	stand volume index; indeks spremembe lesne zaloge
VIF	variance inflation factor

1 INTRODUCTION

Forest stand dynamics represents a rather broad field of research since it implies "the study of changes in forest stand structure with time, including stand behaviour during and after disturbances" (Oliver and Larsen, 1996: 1). Forest stand structure has been recognised as "the physical and temporal distribution of trees and other plants in a stand" with the distribution "described by species, by vertical or horizontal spatial patterns, by size of living and/or dead plants or their parts, including the crown volume, leaf area, stem, stem cross section and others, by plants ages or by combinations of the above" (Oliver and Larsen, 1996: 1). Many different topics can be investigated under the umbrella term of forest stand dynamics. The research of vegetation and species dynamics investigates the phytosociological, successional, and species diversity aspects (Patil and Taillie, 1982; van der Maarel, 2005: 172). The impacts of various natural disturbances on forest stand dynamics are dealt in the studies of natural disturbance patterns (e.g. Pickett and White, 1985; Attiwill, 1994; Frelich, 2002). Finally, changes within forest stands or other plant communities at different spatiotemporal levels are analysed and evaluated in the studies of structural and compositional dynamics (e.g. Bürgi, 1999; Solomon and Gove, 1999; Axelsson et al., 2002; Motta and Garbarino, 2003; Montes et al., 2005; Chapman et al., 2006).

Within a particular natural range of variability, changes in structure and composition of forest stands are a fundamental part of their long-term dynamics (Oliver and Larsen, 1996: 355). Knowledge about past forest stand dynamics is not only crucial for understanding the present structure, but it is also a key issue when directing future development of forest stands (Swetnam et al., 1999; Bončina, 2009: 185, 195). Such knowledge is especially important in ecosystem-based forest management. Besides the changing demands of society on forests, the changing awareness of society regarding the use of renewable natural resources, and better knowledge about other processes in forest ecosystems, knowledge on long-term forest stand dynamics facilitates the evolution of the concept of ecosystem-based forest management (Christensen et al., 1996; Boyce and Haney, 1997; Bončina, 2009: 99). As a representative of ecosystem-based forest management, the concept of close-to-nature forest management is based on mimicry, promotion, hindrance, and the directing of natural processes in forest ecosystems (Franklin, 1993; Diaci and McConnell, 1996; Bončina, 2009). In this regard, it is of great importance to gain detailed knowledge on past forest stand dynamics as well as the processes and factors influencing this dynamics.

The present composition and structure of forest stands are a result of a complex interplay between endogenous and exogenous impact factors differing in their origin and importance.

In the first group of factors, site conditions, natural mortality, inter- and intraspecific relationships, and genetic structure and variability are the most important (Oliver and Larsen, 1996; van der Maarel, 2005), while among exogenous factors, natural and anthropogenic disturbances are the most typical representatives (Anko, 1993; Attiwill, 1994; Oliver and Larsen, 1996; Frelich, 2002).

In the last several centuries, human-induced factors have been far more influential in driving the dynamics of European temperate and boreal forests than natural factors and are changing forest stands to an ever-increasing extent (Linder and Östlund, 1998). Among anthropogenic disturbances, forest management is the most important since it directly and substantially influences the spatiotemporal dynamics of forest stands. However, its impact on forest stand structure and composition and their changes varies significantly in the long-term, depending mainly on the silvicultural system applied at the site (e.g. Sendak et al., 2003; O'Hara et al., 2007). Over the last several centuries, forest management has caused large-scale changes in the spatial distribution, tree species composition, and structure of forest stands in Central Europe (Johann, 2007) and elsewhere (e.g. Linder and Östlund, 1998). In the 18th and 19th centuries, an even-aged, conifer-oriented forestry formed large areas of uniform, mainly Norway spruce (*Picea abies* (L.) Karst.)-dominated forest stands. In contrast, uneven-aged forestry, mainly applied in the 19th and 20th centuries, promoted mixed, more structurally diverse forest stands (Diaci, 2006; Johann, 2007). Differences between both forest management approaches are clearly reflected in the current state of forest stands.

Natural abiotic and biotic disturbances are an integral component of forest ecosystems and, at the same time, are very important impact factors in forest stand dynamics (Pickett and White, 1985; Oliver and Larsen, 1996; Frelich, 2002). Globally, forests are subjected to a variety of natural disturbances, differing in their origin, duration, and extent (Anko, 1993; Attiwill, 1994). They may be one-off, acute events, such as windthrows, snow breakages, or the majority of insect outbreaks, or continuous, chronic events, such as ungulate browsing, pollution, or chronic insect outbreaks (Pickett and White, 1985; Anko, 1993). The effect of natural disturbances on forest stand dynamics may vary over time and space. Different forest types are subjected to different natural disturbance agents. In the mountain forests of Central Europe, wind, snow, bark beetles, and large ungulates were often identified as the main natural disturbance agents (Rottmann, 1985; Gill, 1992b; Ammer, 1996; Schelhaas et al., 2003; Splechtna and Gratzer, 2005; Hanewinkel et al., 2008; Nagel et al., 2007; Jerina, 2008; Firm et al., 2009; Lindner et al., 2010); however, forest fires might play a greater role than previously thought (Schumacher and Bugmann, 2006; Wick and Möhl, 2006; Genries et al., 2009).

Many different investigative methods and data sources are used when examining long-term forest stand dynamics (e.g. Agnoletti and Anderson, 2000). For example, palynology allows the study of vegetation and forest stand composition over several millennia (Šercelj, 1996; Moore et al., 1997). If this method is combined with the analysis of the genetic structure of a forest species population, the analysis can span a time range of 30,000 years (Agnoletti and Anderson, 2000: 16). Another palaeoecological method used when studying long-term dynamics of forest stands is the analysis of charcoal remains in former charcoal-burning sites (Sercelj, 1996; Agnoletti and Anderson, 2000: 15, 79). Dendrochronology makes it possible to reconstruct the development of trees (stands) or natural disturbance patterns within a particular stand over periods spanning several centuries (e.g. Veblen et al., 1994; Schweingruber, 1996; Swetnam et al., 1999; Risch et al., 2003; Nagel et al., 2007; Nagel and Svoboda, 2008; Firm et al., 2009; Genries et al., 2009). Finally, archival data sources, such as forest management plans, forest maps, land registers, felling records, game harvesting records, and other archival data from forest inventories and permanent research plots allow us to reconstruct forest stand dynamics over the past few decades or centuries, to quantify changes in forest structure, and to evaluate the main impact factors (Hladnik, 1991; Swetnam et al., 1999; Agnoletti and Anderson, 2000: 12, 119; Axelsson et al., 2002; Chapman et al., 2006). The abovementioned methods and techniques of forest stand dynamics research are widely used in different research fields of forest ecology and forest history since they provide good insight into the long-term forest stand dynamics and enable a better understanding of the impacts of changing natural and anthropogenic disturbance regimes.

Archival forestry data in written sources were a long-neglected data source in forest stand dynamics research. However, recently they have gained much more attention. They have been used in studies at different spatial scales, from the landscape (e.g. Linder and Östlund, 1998; Radeloff et al., 1999; Axelsson et al., 2002) to the stand level (e.g. Montes et al., 2005; O'Hara et al., 2007), and in different forest types, such as boreal coniferous forests (Linder, 1998; Linder and Östlund, 1998; Axelsson and Östlund, 2001; Axelsson et al., 2002), pine (Cain and Shelton, 2001; Montes et al., 2005), oak (Chapman et al., 2006), mixed deciduous (Bernadzki et al., 1998; Duchesne et al., 2005), and mixed deciduous-coniferous forests (Bončina et al., 2003; Motta and Garbarino, 2003; O'Hara et al., 2007; Schuster et al., 2008; Poljanec et al., 2010; Ficko et al., 2011).

In Central and Southeastern Europe, mixed deciduous-coniferous forests prevail and mountainous silver fir (*Abies alba* Mill.)-European beech (*Fagus sylvatica* L.) forests, in which Norway spruce is often abundantly admixed, are one of the most widespread forest types (EEA, 2006). In Slovenia mountainous silver fir-European beech (hereafter fir-beech) forests represent only 14 % of the total forest cover (Bončina et al., 2002), but exhibit extraordinary ecological and economic forest services. The majority of mountainous fir-beech forests in Slovenia were already more or less intensively exploited in the 17th and 18th centuries, mainly for the production of charcoal and potash used in the iron and glass industries (Veber, 1986; Kordiš, 1993; Prpič, 2001; Perko, 2002; Johann, 2007). Even earlier, from the Middle Ages up to the 17th century, some extensive forest use, such as cattle grazing, slash-and-burn, resin production, and small, uncontrolled cutting, were commonplace in the majority of fir-beech forests (Veber, 1986; Kordiš, 1993; Perko, 2002; Papež and Černigoj, 2007). In the 18th century, regular planned forest management started with the first forest inventories and forest management plans in the Idrija mine-owned forests in 1724 and 1759 (Perko, 2002; Bončina, 2009) and later in forests on the Trnovski gozd plateau (broader Trnovo region) in 1771 (Flamek, 1771), but became widespread at the end of the 19th and at the beginning of the 20th century. At this time, most of the state, church, or landocracy owned forests were inventoried and regulated for the first time, exemplified by the broader region of Snežnik (including Leskova dolina) in the Dinaric Mountains in 1864 or the broader area of Bohinj (including Jelovica) in the Julian Alps in 1880. Some archival forest management plans were lost or destroyed during this long period of time, but the majority of them, or at least the raw data from forest inventories, have been preserved. Thus, archival forest inventory data sources make it possible to evaluate long-term forest stand dynamics of mainly uneven-aged forests and to verify the prevailing opinion that uneven-aged forest stands are generally considered to be stable in terms of structure and composition (e.g. Larsen, 1995), especially when compared with even-aged stands (O'Hara et al., 2007).

There were some simplified opinions and explanations of the long-term dynamics in the fir-beech forest type. These occurred mainly due to a lack of research on this topic in this particular forest type. In Slovenia, few studies have analysed the dynamics of fir-beech forests over the long-term (e.g. Gašperšič, 1967; Bončina, 1999; Firm et al., 2009; Diaci et al., 2010a), and only some attempts have been made to study the variability of the dynamics at the forest stand and landscape spatial levels between geographically diverse study areas (e.g. Bončina et al., 2003). Considering their geographical location, forests within the fir-beech forest type differ in the history of forest management (e.g. Kordiš, 1993), which is reflected in their current structure and composition. Moreover, they also differ in the main influential factors of forest stand dynamics. In Slovenia, there has been much analysis of the different impact factors influencing the current forest stand state or their short-term dynamics (e.g. Wraber, 1950; Veselič, 1991; Koren, 1997; Bončina, 1996; Jarni et al., 2004; Ogris et al., 2004; Papež and Černigoj, 2007), but few studies have investigated their long-term impact on forest stand dynamics (e.g. Papler-Lampe, 2008; Firm et al., 2009; Poljanec et al., 2010;

Ficko et al., 2011).

The objectives of our study were thus:

1) to investigate the dynamics of the structure and composition of mainly uneven-aged fir-beech forests in three spatially dislocated study areas over the last century using archival data, with an additional particular focus on silver fir;
2) to identify the main influential factors and to evaluate their role in driving long-term forest stand dynamics in fir-beech forests in geographically diverse locations;
3) to examine factors influencing the occurrence and severity of natural disturbances as one of the main influential factors in fir-beech forests in the Alps.

To achieve our objectives, we hypothesised that:

1) From the beginning of regular forest management until the present, the tree species composition and diameter distribution of forest stands in Dinaric and Alpine fir-beech forests have been changing. Forest stand dynamics significantly differed between forest areas in the Dinaric Mountains and the Alps. It was substantially influenced by different forest stand states at the beginning of the research period and differences in forest management concepts.
2) At the beginning of regular forest management, the population of silver fir was significantly younger than at present. The present population of silver fir in the alpine fir-beech forest area is younger in its development than the silver fir population in Dinaric fir-beech forests. In the Dinaric fir-beech forests the fluctuations of the main tree species has been more evident than in the fir-beech forests in the Alps.
3) The impact of large ungulates (particularly red deer) on the long-term dynamics of Dinaric fir-beech forests changed during the analysed period due to changes in red deer population densities. In recent decades, red deer has had a fundamental impact on the recruitment of silver fir into the stand canopy.
4) In fir-beech forests in the Alps, natural disturbances (windthrow, snow breakage, and insect attacks) have a significant influence on forest stand dynamics. The occurrence of natural disturbances is significantly influenced by previous occurrences of natural disturbances and by the structure and tree species composition of forest stands.
5) Archival data from old forest management plans make it possible to study forest stand dynamics at different spatial levels – from forest regions to (sub)compartments.

2 SCIENTIFIC PAPERS

2.1 STAND DYNAMICS OF SILVER FIR (*Abies alba* Mill.)-EUROPEAN BEECH (*Fagus sylvatica* L.) FORESTS DURING THE PAST CENTURY: A DECLINE OF SILVER FIR?

Klopčič M., Bončina A. 2011. Stand dynamics of silver fir (*Abies alba* Mill.)-European beech (*Fagus sylvatica* L.) forests during the past century: a decline of silver fir? = [Sestojna dinamika jelovo-bukovih gozdov v zadnjem stoletju: ali jelka nazaduje?]. Forestry, in press

Forestry Advance Access published April 28, 2011

Forestry An International Journal of Forest Research

Institute of Chartered Foresters

Forestry, doi:10.1093/forestry/cpr011

Stand dynamics of silver fir (*Abies alba* Mill.)-European beech (*Fagus sylvatica* L.) forests during the past century: a decline of silver fir?

MATIJA KLOPCIC*, AND ANDREJ BONCINA

Biotechnical Faculty, Department of Forestry and Renewable Forest Resources, University of Ljubljana, Vecna pot 83, 1000 Ljubljana, Slovenia
*Corresponding author. E-mail: matija.klopcic@bf.uni-lj.si

Summary

Uneven-aged silver fir-European beech forests in Slovenia were studied to investigate the dynamics of their structure and composition in three different study areas over the last century, with a particular focus on silver fir dynamics. The study used current and archival data from forest inventories and historic forest management maps for a period of ~110 years. The dynamics of several structural and compositional parameters of the forest stands were also examined using a stand volume index, the Gini coefficient and a recruitment rate index. Substantial changes in diameter growth at breast height structure, stand volume, tree size diversity and tree species composition were documented during the observed period. Additionally, silver fir underwent large-scale changes. Significant differences, as well as some similarities, in forest stand dynamics were observed on a regional spatial scale. These dynamics are underpinned by a complex array of natural and anthropogenic factors; past forest use and the silvicultural systems applied, the impact of large ungulates and site characteristics seem to play important roles.

Introduction

Within a particular natural range of variability, changes in composition and structure are a fundamental part of forest stand dynamics (Oliver and Larsen, 1996: p. 355). Knowledge about past dynamics is crucial to understand the present structure of forest stands and to properly manage forest ecosystems for the future (Swetnam *et al.*, 1999). Structural and compositional changes of forest ecosystems are triggered by numerous factors which differ in their origin and importance (Oliver and Larsen, 1996). In the last several centuries or even millennia, anthropogenic factors have been more influential than natural ones, changing the structure and composition of forest stands to an ever-increasing extent (Linder and Östlund, 1998). Foremost among them is forest management, but the impact on structural and compositional changes of forest ecosystems varies significantly depending on the silvicultural system (e.g. Sendak *et al.*, 2003).

Under the broad conception of forest stand dynamics, many different topics can be investigated using various methods. Research of vegetation and species dynamics (van der Maarel, 2005: p.172) analyses the phytosociological and successional aspects of forest dynamics, and studies of disturbance patterns (Pickett and White, 1985) deal with impact of natural disturbances on forest stand development, while studies of structural and compositional dynamics analyse changes at the landscape (Bürgi, 1999; Axelsson *et al.*, 2002) or, more frequently, forest stand level (Montes *et al.*, 2005; Motta and Garbarino, 2003). Palynological methods (Moore *et al.*, 1997) allow us to study tree species composition over several millennia. Dendrochronological methods (Schweingruber, 1996) make it possible to reconstruct the development of trees over periods spanning several centuries. Finally, methods based on archival data from forest inventories or permanent research plots (Swetnam *et al.*, 1999; Agnolleti and Anderson, 2000) allow us to reconstruct long-term forest stand dynamics over the past few decades or centuries.

The usefulness of past forest inventory data and other archival data is somewhat limited, as methodological differences in inventories are often too significant to allow for stringent scientific analysis, and cautious interpretation of results is indispensable (Agnolleti and Anderson, 2000). Caution is therefore needed in generalizing conclusions, and the transfer of know-how into practice is often limited (Swetnam *et al.*, 1999). Nevertheless, detailed temporally and spatially explicit archival data enable spatio-temporal analysis of structural and compositional changes on the landscape or even forest stand level (Axelsson *et al.*, 2002). Archival data were a long-neglected data source in research of forest stand dynamics on a stand spatial scale, but recently, they have been used in studies of dynamics of boreal (Linder and Östlund, 1998), pine (Montes *et al.*, 2005), oak (Chapman *et al.*, 2006), mixed broadleaf (Bernadzki *et al.*, 1998) and silver fir (*Abies alba* Mill.)-European beech (*Fagus sylvatica* L.)-Norway spruce (*Picea abies* (L.) Karst.) forests (O'Hara *et al.*, 2007).

Mountainous silver fir-European beech forests (hereinafter: fir-beech forest), in which Norway spruce is frequently abundant, represent a significant part of the total forest in Central and south-eastern (SE) Europe (European Environment Agency (EEA), 2006). Mountainous fir-beech forests, representing 14 per cent of the total forest cover in Slovenia (Boncina *et al.*, 2002), are known to have been the late successional forest plant community in the SE part of Europe for the past 7000 years, during which time fir and beech exhibited considerable dynamics (Sercelj, 1996: p. 14; Wick and Mohl, 2006). In the past few decades, decline of fir abundance was significant in these forests and more broadly in Europe (Senn and Suter, 2003; Vrska *et al.*, 2009; Ficko *et al.*, 2010); silver fir decline was recorded throughout Europe in the second half of the twentieth century (Larsen, 1986; Elling *et al.*, 2009), and the species was strongly affected regionally by large ungulate browsing, resulting in lower silver fir growth and a reduction in its abundance in forest stands (Senn and Suter, 2003; Heuze *et al.*, 2005).

Most fir-beech forests were intensively exploited in the seventeenth and eighteenth centuries (Kordis, 1993: p. 14; Prpic, 2001: p. 33 and 529; Johann, 2007). Regular forest management with the first forest inventories started in the eighteenth century (Flamek, 1771) and became widespread in the second half of the nineteenth and beginning of the twentieth century; in most of these forests, uneven-aged silvicultural systems were applied. Archival data of forest inventories thus makes it possible to verify the prevailing opinion that uneven-aged forest stands are generally considered to be stable in terms of structure and composition (Larsen, 1995), which in the long term means negligible fluctuations in the stand volume, diameter growth at breast height (d.b.h.) structure and tree species composition of forest stands. Some studies of uneven-aged forests show the contrary—significant changes in structure and composition of forest stands were found in the long term (e.g. O'Hara *et al.*, 2007). Similarly, there are simplified opinions and explanations of the long-term dynamics of fir-beech forests and fir decline; some studies researched the dynamics of fir-beech forests (Gaspersic, 1967; Korpel, 1995), but there have been few attempts (e.g. Boncina *et al.*, 2003) to study the variability of stand dynamics of the same forest type on both the stand and landscape levels between geographically diverse study areas.

The aim of our study was to investigate the dynamics of the structure and composition of uneven-aged fir-beech forests in three different study areas over the last century using archival data, with a particular focus on silver fir dynamics. We hypothesized that (1) structural and compositional changes of the analysed forest stands in the last century were minor due to applied uneven-aged silvicultural systems; (2) silver fir decline was evident during the study period and (3) forest stands of the same type developed differently depending on past forest use.

Methods

Study area

The present study was carried out in three study areas of fir-beech forest: Jelovica, Trnovo and Leskova dolina (Figure 1). Overuse, forest devastation and the need for permanently productive forest were the reasons behind the early regular forest management in this area; the first forest inventories and forest management plans were made in the eighteenth century (e.g. Flamek, 1771). However, forests in the three study areas differ in past forest use and site characteristics (Table 1).

The Jelovica site is located in the Alps, where extensive logging and charcoal and potash production for ironworks and glassworks started as early as the sixteenth century and were preceded by intensive cattle grazing. In the nineteenth and early twentieth century forest management was based on the theory of maximum land yield, which used clear-cutting and mainly regular shelterwood cutting, combined with the planting of conifers, predominantly spruce. In the 1960s, nature-based silviculture became established, mainly using irregular shelterwood and partly using plenter silvicultural system, a type of selection systems. In the forests of Leskova dolina, located in the Dinaric Mountains, grazing and slash and burn had been practiced as early as the fifteenth century, followed by uncontrolled cutting and severe forest degradation in the eighteenth and nineteenth centuries, and the introduction of plenter forest management in the broader region in the early twentieth century by Schollmayer (Kordis, 1993: p. 37; Klopcic *et al.*, 2010); conifers were preferred over broadleaves and present forests are characterized by a high proportion of conifers, mainly fir. From the 1960s onward, a combination of plenter and small-scale irregular shelterwood silvicultural systems was used. In Trnovo, grazing, charcoal and resin production and uncontrolled cutting were commonplace in the seventeenth century and earlier. After the first forest inventory in 1771, a regular shelterwood silvicultural system was introduced (Flamek, 1771), but after the 1960s, it was changed to an irregular shelterwood system; a plenter system was applied in a minor proportion of forest area.

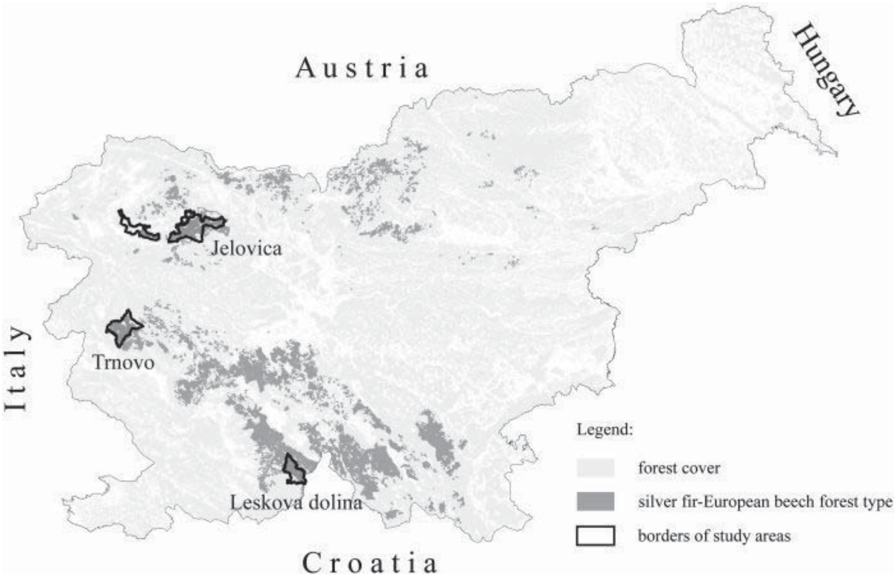

Figure 1. Locations of study areas within the silver fir-European beech forest type in Slovenia.

Table 1: Site and forest stand characteristics of study areas

	Unit	Study area		
		Jelovica	Trnovo	Leskova dolina
Year of the data		2002	2003	2004
Study area	ha	6784	3562	2456
Forest cover	%	97.3	93.5	98.7
Mean compartment area	ha	20.07	12.67	18.75
Elevation	m a.s.l.	480–1760	500–1440	740–1350
Inclination	Degree	20.9	18.2	18.9
Bedrock		Carbonate	Carbonate	Carbonate
Soil type		Eutric cambisols, rendzinas	Eutric cambisols, rendzinas	Eutric cambisols, rendzinas
Mean temperature	°C	5.5	7.7	6.2
Mean annual precipitation	mm	2338	2359	2008
Stand volume—mean	$m^3\ ha^{-1}$	340	328	468
Range (10–90%)	$m^3\ ha^{-1}$	200–484	164–491	403–537
Volume increment	$m^3\ ha^{-1}\ year^{-1}$	7.5	6.6	9.4

Site characteristics in the analysed forest areas vary due to different geographical latitude and orography. Forests in Jelovica are characterized by Alpine vegetation and a naturally higher proportion of spruce compared with the other study areas. For forests in Leskova dolina, Dinaric (Illyric) plant species are characteristic, while in Trnovo, a fir-beech forest type with some characteristics of Dinaric, Alpine and Submediterranean vegetation prevails.

Historical data acquisition and Geographic Information System database creation

Dynamics of forest stands were analysed with archival forest stand data from forest inventories in Forest Management Plans (FMP) and archived forest management maps, both maintained by the Slovenian Forest Service. Detailed forest inventories were typically carried out every 10 years; inventory data from 10, 9 and 8 forest inventories are available for Jelovica, Leskova dolina and Trnovo, respectively (Table 2). Since the first inventories, forests have been divided into a network of basic inventory units (compartments), which has remained largely intact; data on forest stands are shown by compartment with an average area of 12–20 ha (Table 1). Additional explanatory information was gathered from the textual parts of FMPs.

Forest stand data were acquired with multiple inventory methods. Most successive inventories involved full callipering of forest compartments. After the 1970s, but mostly after the 1990s, the method of systematic permanent sampling plots (grid 200 × 200 m or 250 × 500 m, area of a plot = 400 or 500 m^2, N = 1654, 488 and 543 for Jelovica,

Table 2: Years of archival forest management plans used in the study with applied inventory methods and availability of basic data

Study area	Start of validity of forest management plan/used inventory method*/availability of basic data on d.b.h. structure**									
Jelovica	1899	1908	1922	1932	1955	1965	1973	1983	1992	2002
	FC	FC	FC	FC	FC	FC; OA	PSP	PSP	PSP	PSP
	A	NA	NA	NA	PA	NA	A	A	A	A
Trnovo	1897	1907		1931	1952	1963	1973	1983	1993	2003
	FC	FC		FC	FC	FC; OA	FC; OA	FC; OA	PSP	PSP
	NA	NA		A	A	PA	NA	NA	A	A
Leskova dolina		1912		1936	1954	1964	1974	1984	1994	2004
		FC		FC	FC	FC; OA	FC; OA	FC; OA	PSP	PSP
		A		A	A	A	PA	PA	A	A

* Inventory methods: FC, full callipering; OA, ocular assessments of stand volume and tree species composition corrected with data from full callipering; combined with the ocular field description of forest stands.
** Availability of data: A, available for the whole FMU; PA, partly available for some compartments; NA, not available.

Leskova dolina and Trnovo, respectively) was applied, combined with field description of forest stands and basal area measurement (Kovac *et al.*, 2009). In most inventories, all trees above a d.b.h. (1.3 m) of 10 cm were measured, while in some inventories, trees over 16 cm d.b.h. (Jelovica 1899–1932) or 8 cm d.b.h. (Leskova dolina 1912–1936) were measured. In these cases, we converted the data with standard methods (Boncina *et al.*, 2003) to the measurement threshold of 10 cm d.b.h. In the various inventories, the number of trees was divided into d.b.h. classes of different intervals (2-, 5-, 10-cm); 10-cm d.b.h. classes were used to unify the data. Tree species composition of forest stands was calculated as the proportions of the main tree species in the total stand volume. In most FMPs tree species composition was recorded by individual species. However, the 1912 forest inventory for Leskova dolina shows only cumulative data for broadleaves and conifers, but the textual part of the FMP clearly shows that conifers were represented by fir (only individual spruce were present) and broadleaves by beech. The stand volume was calculated from data on number of trees per d.b.h. class and a standard tariff (see Biolley, 1920), which could be used irrespective of tree species or stand type. Missing data on the number of trees were reconstructed using mean d.b.h. structure per hectare for a certain period and original stand volume data from FMPs.

Compartment boundaries shifted slightly in the analysed period. Archival maps from individual periods were therefore scanned. Images were then georeferenced using at least 10 control points per image to do a third order transformation and using resampling methods of bilinear interpoloation or cubic convolution (Minami, 2000). Finally, the georeferenced maps were digitised. Forest inventory data from individual periods were recalculated to present spatial repartition of forests (compartments), and a Geographic Information System (GIS) database at the compartment level was made. ArcMap 9.1 and MapInfo Professional 9.0 software were used for graphic processing and creating the GIS database.

Data analysis

Changes in forest stands were evaluated with selected structural and compositional indicators: d.b.h. structure, stand volume, tree size diversity, tree species composition and recruitment rate.

To evaluate the dynamics of d.b.h. structure, d.b.h. distributions of number of trees per 10-cm d.b.h. class were used.

The dynamics of stand volume was investigated with stand volume (cubic metre per hectare) and a stand volume index (SVI) (Table 3). The SVI is a measure of the relative change in stand volume calculated as the quotient between the stand volume at a particular point in time and the stand volume at the first forest inventory; its values could range from −1 (forest stand was completely removed) to $+\infty$.

The tree size diversity within forest stands was assessed with the Gini coefficient (GC) (see Weiner and Solbrig, 1984; Lexerød and Eid, 2006), which was originally developed to determine inequality in income distributions in economics, but has been also used to measure size hierarchies in plant populations (Weiner and Solbrig, 1984), inequality in a diversity measurement (Patil and Taillie, 1982) and heterogeneity in tree sizes (Lexerød and Eid, 2006; O'Hara *et al.*, 2007). In theory, the GC is defined as the area between the line of perfect equality (the diagonal) and the Lorenz curve, expressed as the proportion of the area under the diagonal (Weiner and Solbrig, 1984). When measuring tree size diversity, the GC requires trees to be ranked by size for its calculation and quantifies the deviation from perfect equality when all trees are of equal size. Tree size diversity is measured on a scale from 0 to 1; the GC would be 0 if all trees in a stand were of equal size, while it would equal 1 if all trees but one had a value of 0. A higher and more constant GC indicates more uneven-sized forest stands, while GC values near 0 indicate an even-sized structure of forest stands (O'Hara *et al.*, 2007). When assessing structural diversity, the use of basal area or volume may provide a more accurate estimation of structural diversity than the use of the number of trees (Solomon and Gove, 1999). Therefore, in our study, the GC was calculated using the data on number of trees and their basal area per d.b.h. class (Lexerød and Eid, 2006; O'Hara *et al.*, 2007) by compartment when full callipering had been done, while for inventories after 1970, but mostly after 1990, the data from permanent sampling plots, on which 10 or more trees were recorded, were used. In cases when less than 50 trees on a

Table 3: Indices for investigating dynamics of structural and compositional parameters of forest stands

Index	Equation
SVI	$\mathrm{SVI}_{i,y} = \left(\dfrac{\mathrm{SV}_{i,y} - \mathrm{SV}_{i,\mathrm{yold}}}{SV_{i,\mathrm{yold}}}\right)$
GC (Lexerød and Eid, 2006)	$\mathrm{GC}_y = \dfrac{\sum_{j=1}^{n}(2j-n-1)\cdot \mathrm{ba}_j}{\sum_{j=1}^{n}\mathrm{ba}_j\cdot(n-1)}$
Recruitment Rate Index (RRI) (Yoshida *et al.*, 2006)	$\mathrm{RRI}_i = \left(\dfrac{\left(N_{\mathrm{yold}} + \mathrm{Nrec}_{i,y}\right)}{N_{\mathrm{yold}}}\right)^{0.1} - 1$

i, group of tree species or individual tree species; *y*, year of studied forest inventory; yold, year of first/previous forest inventory; SV, stand volume; *j*, rank of a tree in ascending order from 1 to *n*; *n*, total number of trees; ba, basal area ($\mathrm{m}^2\ \mathrm{ha}^{-1}$) of a tree; Nrec, number of recruited trees over measuring threshold of 10 cm d.b.h. per PSP; N_{yold}, number of all measured trees in first measurement on PSP.

permanent sampling plot (PSP) (or in a compartment) were present, the calculated GC was corrected by the quotient $n/(n-1)$ to reduce the bias caused by a small sample size (Weiner and Solbrig, 1984; Dixon *et al.*, 1987).

Further, the dynamics of tree species composition were assessed for a change in the share of individual tree species in the total stand volume of forest stands. d.b.h. distributions per tree species and recruitment rate index (RRI) (Table 3), which was adopted after Yoshida *et al.* (2006), were used to forecast the future development of forest stands and fir specifically.

Statistical differences in d.b.h. distributions of forest stands as well as of fir between study areas in studied periods were examined using a χ^2-test (Zar, 2010: p. 470). Additionally, differences between study areas in means and changes of SVI, GC and RRI were analysed by the non-parametric Kruskal–Wallis test and *post hoc* multiple comparisons of ranks for groups by using *z*-values (Zar, 2010: p. 214).

Results

Changes in the structure and composition of forest stands

The d.b.h. structure of forest stands changed noticeably in the analysed period (Figure 2); in general, the number of large-diameter trees (d.b.h. ≥ 50 cm) and, in most cases,

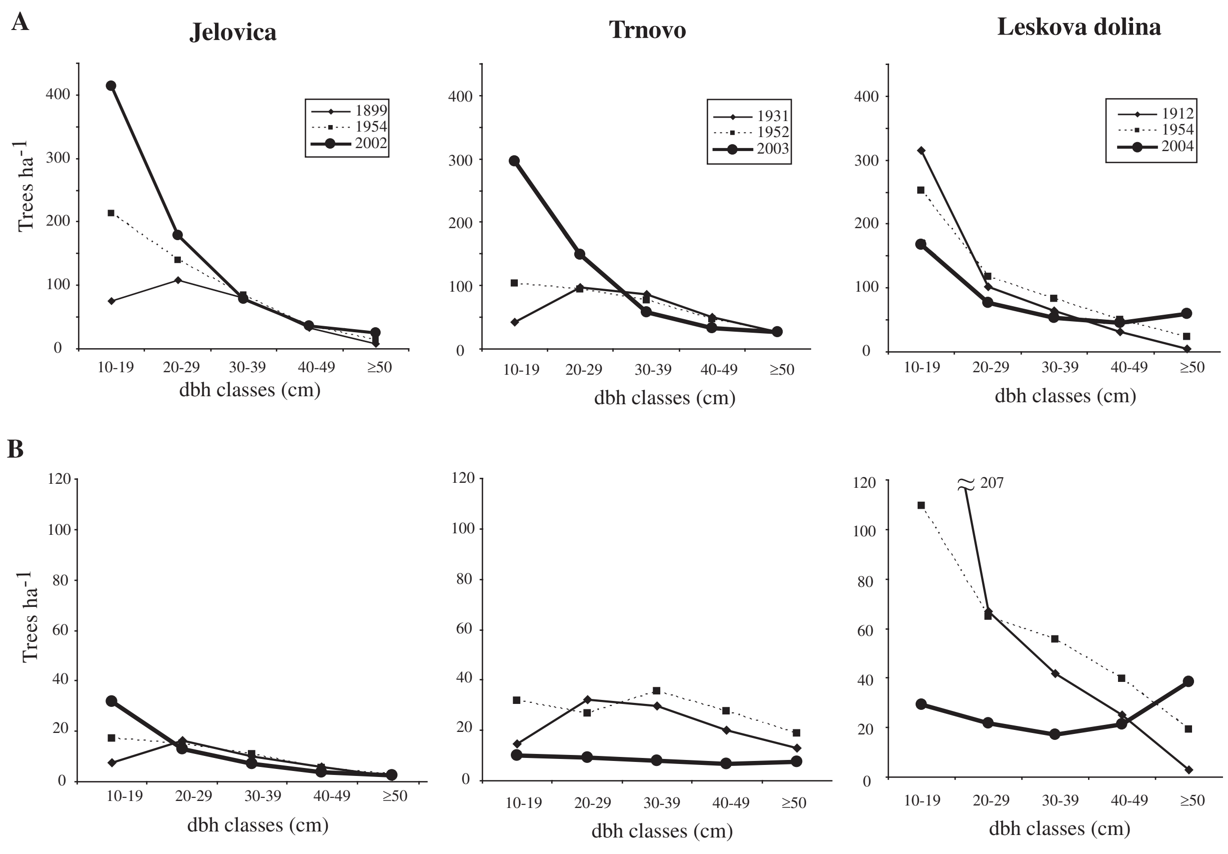

Figure 2. Dynamics of d.b.h. distributions in studied forest stands (A) and silver fir population (B).

the total number of trees increased. However, changes in d.b.h. structure varied significantly between study areas (χ^2-tests: all $P < 0.01$). At the start of study period, the total number of trees in Jelovica and Trnovo was low (304 ha^{-1} and 303 ha^{-1}, respectively), while in Leskova dolina, stand densities in 1912 were the highest in the studied period (518 ha^{-1}). The development of the d.b.h. structure of forest stands in Leskova dolina clearly showed a shift in diameter distribution towards large-diameter trees; in the studied period, the number of large-diameter trees (d.b.h. ≥ 50 cm) increased by 54 trees ha^{-1} and the number of small-diameter trees (d.b.h. = 10–29 cm) dropped by 171 trees ha^{-1}. Conversely, in Jelovica and Trnovo, the number of small-diameter trees rose substantially in the studied period, by 409 trees ha^{-1} and 307 trees ha^{-1}, respectively.

Changes in d.b.h. structure reflect an increase of stand volume of forest stands in the study period (Figure 3). SVI varied significantly among study areas over time (Kruskal–Wallis tests (hereafter KW): all $P = 0.000$). However, despite differences in d.b.h. structure, the stand volume in the study period increased in all study areas, by 1.6-, 1.6- and 2.4-fold in Jelovica, Trnovo and Leskova dolina, respectively.

Tree size diversity (GC) significantly differed between study areas in all 10-year periods (KW: all $P < 0.01$), and

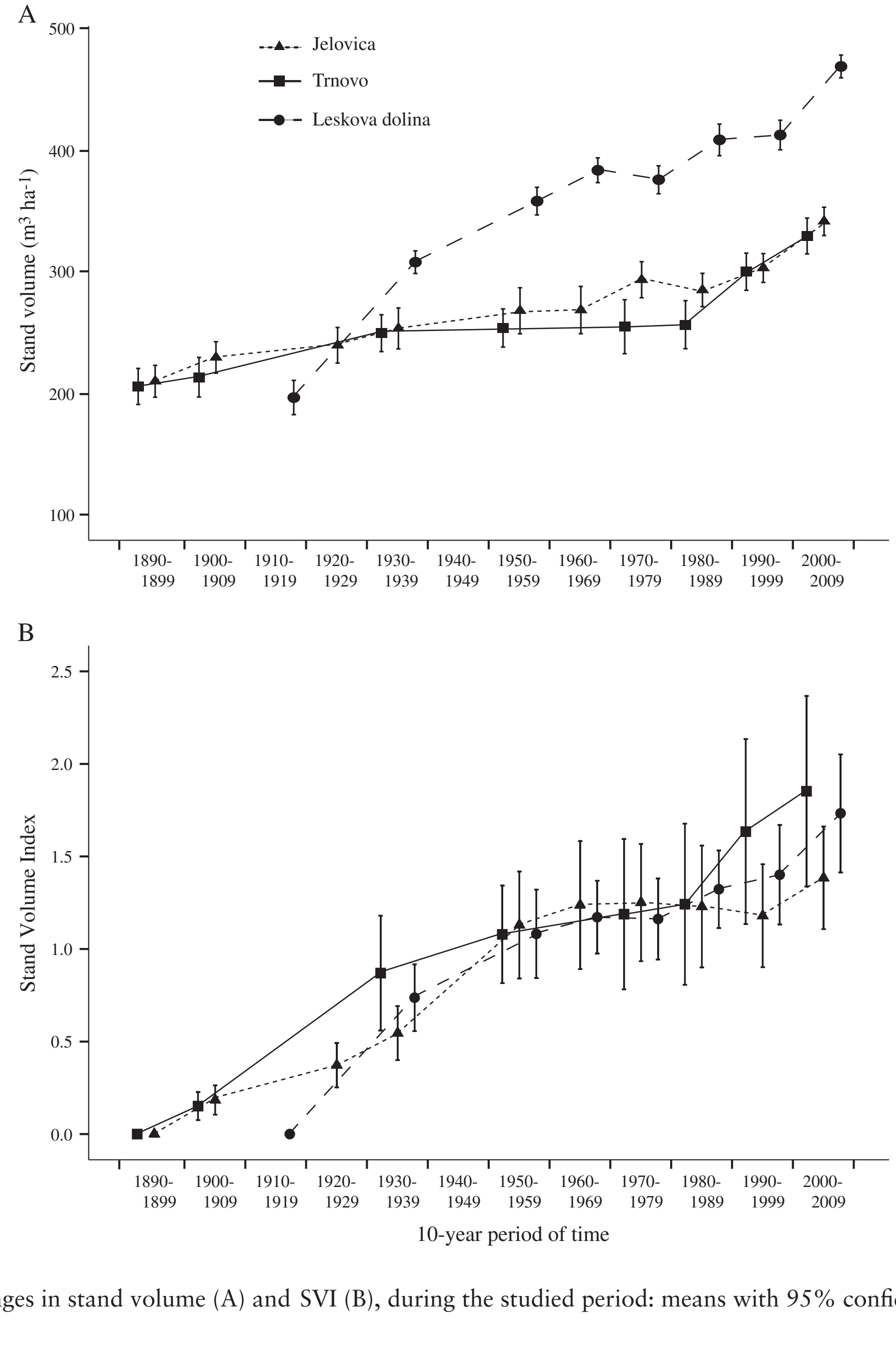

Figure 3. Changes in stand volume (A) and SVI (B), during the studied period: means with 95% confidence intervals.

the GC's dynamics were noticeably distinguished between study areas (Figure 4). Forest stands in Jelovica changed from stands with the highest tree size diversity at the beginning of the observation period to stands with the lowest tree size diversity at the end of the observation period; the GC decreased 1.6-fold in the period 1899–2002. On the contrary, the tree size diversity of forest stands in Trnovo underwent only minor changes. In Leskova dolina, the GC increased to 0.51 by the 1960s and only slightly decreased afterwards; a clear trend of forest stands becoming more diverse in their tree size diversity was observed there.

The tree species composition of the studied forests underwent profound changes in the study period (Table 4). Major fluctuations of coniferous and broadleaved tree species were observed; in the last decades, the proportion of broadleaves and spruce increased significantly, while a decrease in the proportion of fir was observed.

Differences in tree species proportions between study areas were statistically significant in all studied 10-year periods (KW: all $P < 0.01$). In Jelovica, spruce was the dominant tree species throughout the study period, representing more than two-thirds of total stand volume, while the already low proportion of fir almost halved in the 1899–2002 period. In Trnovo, fluctuations of dominant tree species were recorded: beech was the dominant species (57 per cent) in 1931, fir in 1963 (54 per cent) and beech again in the 1980s (51 per cent). The proportion of fir constantly declined after 1963 and the proportion of beech and spruce increased. In Leskova, dolina fir was the dominant species throughout the study period, but its proportion dropped by 16 per cent in the 1964–2004 period; the proportions of beech and spruce substantially increased in the studied period.

The recruitment rate of all tree species was generally sufficient; on average, 147.3 ± 11.5 trees ha^{-1} 10 $year^{-1}$ (mean ± 1.96 × $SE/\sqrt{n}$) were recruited to the canopy of the analysed forest stands in the last inventory period, with spruce being the most successful (87.1 ± 9.1 trees ha^{-1} 10 $years^{-1}$).

However, the RRI significantly differed between study areas (Figure 5; KW: $P = 0.000$); the RRI in Jelovica was significantly higher than the RRI in Trnovo and Leskova dolina (*post hoc* tests: both $P = 0.000$), while differences were not significant between Trnovo and Leskova dolina (*post hoc* tests: $P = 0.686$). Spruce had the highest recruitment rate in Jelovica and Leskova dolina (RRI = 0.019 and RRI = 0.009, respectively), while in Trnovo, the RRI was the highest for beech (RRI = 0.008). Fir had a significantly lower RRI than the other main tree species in all three study areas (KW and *post hoc* tests: all $P = 0.000$).

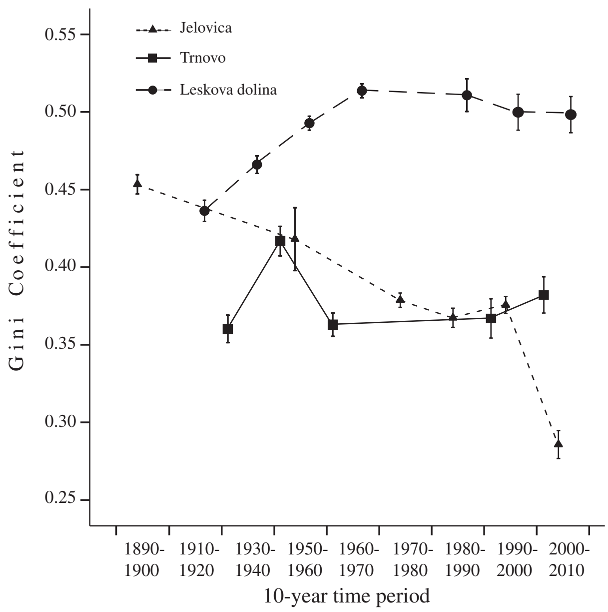

Figure 4. The tree size diversity in the studied forest stands: means of the GC with 95% confidence intervals.

Dynamics of the silver fir population

Changes in the d.b.h. structure of fir were profound in the studied period (Figure 2); furthermore, d.b.h. structures

Table 4: Changes in tree species composition in the studied period (proportions are based on total stand volume)

Study area	Tree species	10-year time period 1890–1900	1911–1920	1931–1940	1951–1960	1961–1970	1981–1990	1991–2000	2001–2010
Jelovica	Silver fir	16	–	–	–	–	13	9	9
	Norway spruce	68	–	–	82*	–	70	75	73
	European beech	16	–	–	18*	–	17	14	16
	Other species	0	–	–	–	–	0	2	2
Trnovo	Silver fir	41*	–	38	49	54	37	26	18
	Norway spruce	–	–	4	6	6	10	11	15
	European beech	59*	–	57	44	37	51	59	62
	Other species	–	–	1	1	3	2	4	5
Leskova dolina	Silver fir	–	68*	–	68	69	62	57	53
	Norway spruce	–	–	–	9	10	12	17	18
	European beech	–	32*	–	18	17	22	23	26
	Other species	–	–	–	5	4	4	3	3

* The data were available only for groups of coniferous and broadleaved tree species.

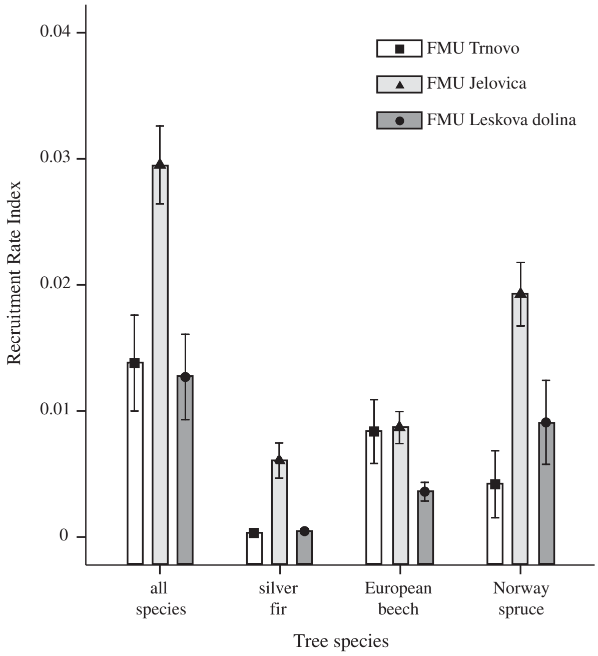

Figure 5. Recruitment rate of the main tree species: means of the RRI with 95% confidence intervals.

significantly differed between study areas in all 10-year periods (χ^2-tests: all $P < 0.01$). In Jelovica, the total number of fir in forest stands increased from 42 to 58 fir ha^{-1} in 1899–2002. Additionally, thin trees became prevalent in the fir population: the proportion of fir with d.b.h. = 10–19 cm increased 4.2-fold in the period 1899–2002, while the proportion of fir with d.b.h. = 20–49 cm dropped 1.4-fold. Conversely, the total number of fir in Trnovo and Leskova dolina dropped by 68 and 217 fir ha^{-1}, respectively. In Trnovo, the number of fir declined in all d.b.h. classes; the steepest decline was recorded in small-diameter (d.b.h. = 10–29 cm) and medium-diameter (d.b.h. = 30–49 cm) fir (2.4- and 3.4-fold, respectively). In Leskova dolina, the number of small- and medium-diameter fir dropped 5.4- and 1.7-fold, respectively, and the number of large-diameter fir (d.b.h. ≥ 50 cm) increased 12.7-fold.

The proportion of fir in the tree species composition in the analysed forest stands decreased significantly after the 1960s (Table 4); however, the intensity of this decrease differed between study areas. In Jelovica, fir had a low proportion throughout the studied period and it continued to decline; it declined by 4 per cent in 1983–2002. Conversely, in Trnovo and Leskova dolina, fir was the dominant tree species in the 1950s and 1960s, whereupon, its proportion fell by as much as 36 per cent in Trnovo from 1963 to 2003. In Leskova dolina, fir is still the dominant species, but its proportion has been constantly decreasing at a rate of ~5 per cent per decade.

Additionally, the average recruitment rate of fir was very low (13.5 ± 1.3 trees ha^{-1} 10 year^{-1}) and significantly lower compared with beech and even more so compared with spruce (KW, *post hoc* tests: both $P = 0.000$). The RRI of fir (Figure 5) differed significantly between study areas (KW: $P = 0.000$). The highest RRI was recorded in Jelovica (*post hoc* test: both $P = 0.000$); in a 10-year period, 20.8 ± 2.0 fir ha^{-1} were recruited. The RRI of fir in Jelovica was 19 and 13 times higher than in Trnovo and Leskova dolina, respectively. Significant differences were not detected in RRI between Trnovo and Leskova dolina (*post hoc* test: $P = 0.732$), where only 0.8 ± 0.3 fir ha^{-1} 10 year^{-1} and 3.0 ± 0.6 fir ha^{-1} 10 year^{-1}, respectively, were recruited to forest stands. Even though it was the highest among study areas, the RRI of fir in Jelovica was still 3.4 and 1.4 times lower than the RRI of spruce and beech, respectively; even greater differences were observed in Trnovo (13.1 and 26.1 times lower than the RRI of spruce and beech, respectively) and Leskova dolina (19.5 and 7.7 times lower than the RRI of spruce and beech, respectively).

Discussion

Historical data sources enable reconstruction of forest stand dynamics and evaluation of its main influential factors (Agnolleti and Anderson, 2000; Montes *et al*., 2005; Chapman *et al*., 2006). However, cautious interpretation of the results is needed in making conclusions when using archival data (Swetnam *et al*., 1999) since they provide only single snapshots of forest stands at a certain point in time (Axelsson *et al*., 2002). One snapshot of a forest stand is only one of many—albeit perhaps noteworthy and different—states in time over the development of a forest stand in the long term. Compared to palynological and dendrochronological methods of forest stand dynamics research, methods based on archival records enable an investigation of forest stand dynamics in a relatively short time period, but they can provide high-resolution data on structural and compositional parameters of forest stands at a certain point in time (Axelsson *et al*., 2002). However, with a large enough density of such forest stand snapshots, it is possible to reconstruct the dynamics of forest stands in detail over a reasonably long period of time.

A variety of forest stand dynamics have been observed in different forest types (e.g. Leak and Filip, 1977; Linder and Östlund, 1998; Motta and Garbarino, 2003; Chapman *et al*., 2006; O'Hara *et al*., 2007); their common characteristics were fluctuations in tree species composition and d.b.h. structure of forest stands. In the past, forest stands were considered to be stable in their structure and composition in the long term (Oliver and Larsen, 1996: p. 355), and this belief was especially strong concerning uneven-aged stands (Larsen, 1995). However, the present study concluded the opposite: over a 110-year period considerable changes were demonstrated in the diameter distribution of trees, stand volume, tree species composition and tree size diversity in our study. Moreover, significant differences, as well as some similarities, in forest stand dynamics were observed on a regional spatial scale inside the same fir-beech forest type.

The main common characteristic of the analysed forest stands was an increase in stand volume, which was mainly a consequence of management decisions from the beginning of the twentieth century until the 1980s to increase stand volume after heavy exploitation of forests in the eighteenth and nineteenth centuries (Gaspersic, 1967; Kordis, 1993: p. 14). An increase in stocking of uneven-aged forest stands has been widespread in the last few decades, with environmental effects and low-intensity forest management being the main causes (e.g. Cavlovic, 2000; O'Hara *et al.*, 2007). The first factor was underpinned by the fact that stocking increases were also reported from even-aged and old-growth forests (e.g. Linder, 1998; Cain and Shelton, 2001; Schuster *et al.*, 2008), while intensive uneven-aged forest management preserved stocking at approximately the same level in the long term (Cain and Shelton, 2001; Yoshida *et al.*, 2006), which confirms the second stated factor.

Diverse dynamics in tree size diversity within forest stands was observed in the study areas. The GC increased in Leskova dolina, stagnated in Trnovo and decreased in Jelovica. Dynamics of tree size diversity similar to those in Leskova dolina and Trnovo were observed in uneven-aged fir-beech-spruce forest stands in Switzerland between 1905 and 1999 (O'Hara *et al.*, 2007). The lower tree size diversity (more even-sized stands) in Jelovica at the end of the observation period was probably a consequence of past forest management that was mainly based on regular shelterwood cutting, but also clear-cutting combined with the planting of spruce. However, not only the mentioned cutting types but even the plenter silvicultural system may sometimes lead to the homogenization of forest stand structure in the long term (Angers *et al.*, 2005). But even if the GC was found to be superior to some other diversity indices in the assessment of diameter diversity (Lexerød and Eid, 2006), the shortcomings of the GC have to be greatly considered. Diverse stand structures with different Lorenz curves (i.e. diameter distributions) can produce the same GC value (Weiner and Solbrig, 1984). Therefore, when interpreting the GC, Lorenz curves have to be considered simultaneously with the GC. In addition, the calculated GC would be a biased estimator of the true tree size diversity if the diameter distribution was highly skewed or the sample size was small (Weiner and Solbrig, 1984; Dixon *et al.*, 1987). In our study, the latter was mainly the case with the data from PSPs; therefore, the correction of GC was used to reduce the bias.

Changes in the d.b.h. structure of the analysed forest stands in the three study areas indicate two different directions of forest development: an increase in stand densities and quantity of small-diameter trees (regeneration of stands) or, more worryingly, an increase in quantity of large-diameter trees (ageing of stands) combined with reduction in the number of trees. Leskova dolina is an example of the latter: a planned increase in stocking together with high browsing pressure of large herbivores (Klopcic *et al.*, 2010) led to a decrease in the total number of trees due to a lack of tree recruitment and a shift of the diameter distribution towards large-diameter trees. The latter could be equated to the ageing process of forest stands since the overstorey (large-diameter) trees were found to be older than the understorey (small-diameter) fir and spruce trees despite the possible suppression of thin fir and spruce over a long period of time (Ferlin, 2002). Similar stand dynamics were documented in many other fir-beech forests in Slovenia (Boncina *et al.*, 2003), in neighbouring Croatia (Cavlovic, 2000) and in the Carpathians (Vrska *et al.*, 2009), as well as in other forest types, e.g. mixed northern coniferous forests in Michigan, USA (Frelich and Lorimer, 1985); mixed loblolly and shortleaf pine in Arkansas, USA (Cain and Shelton, 2001), and oak-dominated forests in New York State, USA (Schuster *et al.*, 2008).

Additionally, substantial changes in tree species composition of the studied forest stands, which significantly differed between study areas, were established in the studied period. Compositional changes of uneven-aged forest stands were frequently reported (Boncina *et al.*, 2003; Sendak *et al.*, 2003; Yoshida *et al.*, 2006), but they were also documented in even-aged and old-growth forests (Bernadzki *et al.*, 1998; Linder, 1998; Bürgi, 1999; Chapman *et al.*, 2006; Schuster *et al.*, 2008; Diaci *et al.*, 2010). General common characteristics of the studied forest stands were a decrease in the fir proportion and increase in the proportion of broadleaves and spruce, particularly in the last four decades. These findings may correspond to the 'natural process' of the alternation of dominant tree species (e.g. Korpel, 1995: p. 230) or more probably to fluctuations in dominance between the main tree species (Sercelj, 1996: p. 62; Wick and Mohl, 2006; Vrska *et al.*, 2009; Diaci *et al.*, 2010). In mixed fir-beech-dominated forest stands, fir was reported to be potentially replaced by spruce (Heuze *et al.*, 2005) or beech (Gaspersic, 1967), which was also partly confirmed in the present study. However, reciprocal or self-replacement of fir and beech in fir-beech forests is significantly influenced by the canopy gap size (Nagel *et al.*, 2010) created by natural or anthropogenic disturbances.

In the studied period, major fluctuations in dominance between fir and beech were most significant in Trnovo, where they had occurred in several decades. A similar process occurred in Leskova dolina; however, our results did not show it distinctly; the time cycle of major fluctuations seemed to be longer there (Gaspersic, 1967; Klopcic *et al.*, 2010). In contrast, in fir-beech forests in the Alps, spruce was the dominant tree species of forest stands throughout the entire studied period. However, the application of an irregular shelterwood silvicultural system after the 1960s caused gradual changes in tree species composition, which is evident in the decreasing proportion of fir in the stand volume and the increasing proportion of broadleaves, beech in particular. Similar changes in tree species composition were also documented in old-growth forest remnants of the studied forest type, but to a lesser extent than in our study areas (e.g. Korpel, 1995: p. 230; Diaci *et al.*, 2010) and in old-growth reserves of other forest types (e.g. Bernadzki *et al.*, 1998; Linder, 1998).

Silver fir, one of the main tree species of the fir-beech forest type and an important species of Central European forests in general (Senn and Suter, 2003; EEA, 2006), underwent the most large-scale changes. Analysis of the d.b.h. structure of fir showed two countervailing dynamics: the fir population in fir-beech forests in the Alps is becoming 'younger' and the fir population in Dinaric fir-beech forests is becoming significantly 'older'. In the Alps (Jelovica), an increase in the number of small-diameter fir is a consequence of the low browsing pressure of large herbivores (Jerina, 2008) and the introduction of the irregular shelterwood system with a long regeneration period with several regeneration fellings, which is favourable for regeneration of shade-tolerant tree species such as beech and fir and less so for the less shade-tolerant spruce (Sendak *et al.*, 2003; Stancioiu and O'Hara, 2006). However, the seed bank of spruce is so extensive that spruce still predominates in the regeneration. Nevertheless, a further increase in fir recruitment rate could be expected in these forest stands since fir represents a considerable proportion of the regeneration (Slovenia Forest Service, unpublished data). In the Dinaric Mountains (Leskova dolina), the quantity of large-diameter fir increased substantially, but insufficient recruitment (Klopcic *et al.*, 2010) caused a decline in the proportion of small-diameter fir. The same changes in the fir population were also observed in Croatia (Cavlovic, 2000), the Italian Alps (Motta and Garbarino, 2003) and the Carpathians (Vrska *et al.*, 2009). Population ageing due to lack of recruitment was also reported for other tree species, including *Tsuga canadensis* (L.) Carr. in mixed forests in Michigan, USA (Frelich and Lorimer, 1985).

An excess of mortality rate over recruitment rate reduced the fir proportion in tree species composition of fir-beech forests in the studied period, insignificantly in the Alps and significantly in the Dinaric Mountains. A reduction in the proportion of fir in mixed forest stands and even a decrease in its spatial distribution has been reported in many European countries (e.g. Cavlovic, 2000; Senn and Suter, 2003; Ficko *et al.*, 2010). The low recruitment rate of fir compared to the other main species (beech and spruce) indicates a general continued decline in the proportion of fir in fir-beech forests; in the next few decades, the proportion of fir may be expected to increase only in fir-beech forest stands in the Alps, which has already been reported in mixed fir-broadleaved forests in the Italian Alps (Motta and Garbarino, 2003).

The observed dynamics of the studied forest stands is underpinned by the complexity of natural and mainly (direct or indirect) anthropogenic factors which work at different spatio-temporal scales (Bürgi, 1999; Sendak *et al.*, 2003; Wick and Mohl, 2006; Vrska *et al.*, 2009; Diaci *et al.*, 2010). Differences in past forest management, browsing pressure and site conditions seem to be the most important factors.

Past forest use, such as charcoal and potash production and forest grazing, changed the studied forest stands to a considerable degree even before the first forest inventories were made. Consequently, the baseline state of studied forest stands differed significantly when the first forest inventories were made, which affected dynamics of forest stands in the studied period. During the studied period, the forest management regime seemed to be an important factor of forest stand dynamics; many researchers found that the current forest structure and composition reflect the use of different silvicultural systems (Leak and Filip, 1977; Sendak *et al.*, 2003; Montes *et al.*, 2005; Yoshida *et al.*, 2006). In our research, all study areas differed in their stand dynamics, and this was mainly due to differences in past forest management. In Jelovica, changes in tree species composition over the studied period reflect forest management in the Alpine area (Johann, 2007) characterized by large-scale cutting, the planting of spruce and the weeding out of beech and other broadleaves. Over the last century, this has led to the present tree species composition of forests, with spruce abundance significantly higher than 'natural' (Veselic and Robic, 2001). Regeneration of forest stands and changes in tree species composition in the Trnovo study area are the result of an irregular shelterwood system with regeneration cuttings on areas of up to 1 ha, which promoted regeneration of shade-tolerant beech and less shade-tolerant spruce. This type of regeneration is obviously not very suitable for shade-tolerant silver fir (see also Leak and Filip, 1977; Stancioiu and O'Hara, 2006), as its proportion is declining, and its recruitment rate is low. The plenter system used in Leskova dolina promoted fir and other conifers in the first five decades of the studied period (Gaspersic, 1967; Klopcic *et al.*, 2010); however, insufficient recruitment of trees, especially of fir —mainly due to high browsing pressure of large herbivores and partly due to increased stocking—resulted in the ageing of forest stands, mainly the fir population. A combination of the plenter system and small-scale irregular shelterwood system was applied after the 1960s, which, together with a significant reduction of large herbivore densities, resulted in a higher recruitment rate of beech and spruce, but not of fir. Just as Frelich and Lorimer (1985) pointed out for *Tsuga canadensis* (L.) Carr. in Michigan, USA, and Linder (1998) for *Pinus sylvestris* L. and Norway spruce in Sweden, there is a great possibility that fir needs a 'window of opportunity'—a co-occurrence of appropriate conditions, i.e. low densities of large herbivores, full- and partial-seed years or natural or anthropogenic disturbances creating different-sized canopy openings (Nagel *et al.*, 2010)—for abundant regeneration and successful recruitment into the forest stand canopy (Senn and Suter, 2003).

In addition to past forest management, browsing by large ungulates (Gill, 1992), but also domestic stock grazing (Vrska *et al.*, 2009), can have a substantial impact on the structure and composition of forest stands in the long term. Differences in large ungulate densities between study areas were obvious (Jerina, 2008). Over the entire observed period, red deer (*Cervus elaphus* L.) density was highest in Leskova dolina, where it reached 5.8 animals km^{-2} in the late 1970s and subsequently decreased to the current 3 animals km^{-2} (Klopcic *et al.*, 2010). Densities were much lower in Jelovica and Trnovo, where the average densities in 2004–2008 were 1.8 and 0.3 red deer km^{-2}, respectively (Jerina, 2008). Many researchers emphasized that large ungulates have been one of the crucial factors driving the changes in tree species composition of Central European forests in the twentieth century (e.g. Gill, 1992; Heuze *et al.*, 2005). Moreover, differences in their regional densities may substantially contribute to the diversity in forest stand dynamics inside the same forest type (e.g. Senn and Suter, 2003; Jerina, 2008).

Site is the most important natural factor; site characteristics significantly affect structure and 'natural' tree species composition, which may vary significantly within the same forest type due to microsite and mesosite differences (Oliver and Larsen, 1996: p. 176 and 372; van der Maarel, 2005: p. 258). In 'natural' tree species composition of fir-beech forests in the Alps, the proportion of fir is slightly lower than in fir-beech forests in the Dinaric Mountains. In contrast, in the Alps, the proportion of spruce in 'natural' fir-beech forests may be three times that in the Dinaric Mountains (Veselic and Robic, 2001).

Factors other than those discussed may also significantly impact the dynamics of mixed forest stands, e.g. natural disturbances (Pickett and White, 1985), differences in competitiveness and natural resource usage between the main tree species (Oliver and Larsen, 1996: p. 14; van der Maarel, 2005: p. 208), the impact of climate change (Lindner *et al.*, 2010) and the introduction and spread of non-native species (Schuster *et al.*, 2008). Furthermore, the dynamics of fir populations could be influenced by additional factors, including inter- and intra-specific relationships, such as autoinhibition and allelopathic relationships between tree species (Oliver and Larsen, 1996: p. 181) or fir decline caused by lack of genetic variability (Larsen, 1986) or pollution (Elling *et al.*, 2009).

Forests will never be structurally or compositionally stable because they continuously respond to changes in their environment (Bernadzki *et al.*, 1998). The forest management regime has a significant impact on change in forest stands. Uneven-aged forest management is often intended to promote 'natural' structures and tree species composition of forest stands. But our study highlights that it is inappropriate to consider tree species composition or structure of uneven-aged forest stands as static. Instead, our goal should be a better understanding and sensible management of dynamics of forest stands, which are the result of a complex interaction of natural and anthropogenic factors at different spatio-temporal levels. Impacts of some factors may change quickly and significantly in spatio-temporal terms (e.g. disturbances, market conditions); the question that arises is what kinds of changes in tree species composition or structure are appropriate or admissible? Large changes typically increase management risks. It therefore makes sense to follow the 'natural' patterns in forest stand dynamics, which may differ within the same forest type and, owing to the unpredictability of the future, can only be partially redirected with forest management.

Funding

Slovenian Research Agency (1000-06-310156).

Acknowledgements

The authors wish to thank Franci Cergolj, Andrej Gartner, Marko Gasperin, Edo Kozorog, Ales Poljanec, Janez Skerbec and Marko Udovic from the Slovenia Forest Service for providing historical data sources and helping with the creation of the database. The comments of the reviewers significantly improved the earlier version of the manuscript.

References

Agnolleti, M. and Anderson, S. 2000 *Methods and Approaches in Forest History*. CABI Publishing, Wallingford, CT.

Angers, V.A., Messier, C., Beaudet, M. and Leduc, A. 2005 Comparing composition and structure in old-growth and harvested (selection and diameter-limit cuts) northern hardwood stands in Quebec. *For. Ecol. Manage.* **217**, 275–293.

Axelsson, A.L., Ostlund, L. and Hellberg, E. 2002 Changes in mixed deciduous forests of boreal Sweden 1866–1999 based on interpretation of historical records. *Landscape Ecol.* **17**, 403–418.

Bernadzki, E., Bolibok, L., Brzeziecki, B., Zajaczkowski, J. and Zybura, H. 1998 Compositional dynamics of natural forests in the Białowieza National Park, northeastern Poland. *J. Veg. Sci.* **9**, 229–238.

Biolley, H. 1920 *L'aménagement des forêts par la méthode expérimentale et spécialement la méthode du contrôle*. Paris Attinger frères, Neuchatel, France.

Boncina, A., Diaci, J. and Cencic, L. 2002 Comparison of the two main types of selection forests in Slovenia: distribution, site conditions, stand structure, regeneration and management. *Forestry*. **75**, 365–373.

Boncina, A., Gaspersic, F. and Diaci, J. 2003 Long-term changes in tree species composition in the Dinaric mountain forests of Slovenia. *Forest Chron.* **79**, 227–232.

Bürgi, M. 1999 A case study of forest change in the Swiss lowlands. *Landscape Ecol.* **14**, 567–575.

Cain, M.D. and Shelton, M.G. 2001 Natural loblolly and shortleaf pine productivity through 53 years of management under four reproduction cutting methods. *South J. Appl. For.* **25**, 7–16.

Chapman, R.A., Heitzman, E. and Shelton, M.G. 2006 Long-term changes in forest structure and species composition of an upland oak forest in Arkansas. *For. Ecol. Manage.* **236**, 85–92.

Cavlovic, J. 2000 Novi program gospodarjenja za G.J. "Belevine 2000–2009—zaustavljanje neponovljivih trendova i iniciranje povoljnih procesa u "razvoju" preborne sume? (in Croatian). *Sumarski list*. **124**, 450–457.

Diaci, J., Rozenbergar, D. and Boncina, A. 2010 Stand dynamics of Dinaric old-growth forest in Slovenia: are indirect human influences relevant? *Plant Biosyst.* **144**, 194–201.

Dixon, P.M., Weiner, J., Mitchell-Olds, T. and Woodley, R. 1987 Bootstrapping the Gini coefficient of inequality. *Ecology*. **68**, 1548–1551.

EEA 2006 *European Forest Types: Categories and Types for Sustainable Forest Management Reporting and Policy. EEA Technical Report, No 9/2006*. European Environment Agency, Copenhagen.

Elling, W., Dittmar, C., Pfaffelmoser, K. and Rötzer, T. 2009 Dendroecological assessment of the complex causes of decline and recovery of the growth of silver fir (Abies alba Mill.) in Southern Germany. *For. Ecol. Manage.* **257**, 1175–1187.

Ferlin, F. 2002 The growth potential of understorey silver fir and Norway spruce for uneven-aged forest management in Slovenia. *Forestry*. **75**, 375–383.

Ficko, A., Poljanec, A. and Boncina, A. 2010 Do changes in spatial distribution, structure and abundance of silver fir (*Abies alba* Mill.) indicate its decline? *For. Ecol. Manage.* **261**, 844–854.

Flamek, F. 1771 *Holz-Schätz oder Überschlagung auch Geometrische Einteilung in die Stallungen oder Järliche Gehausammentlicher Ternovaner Landesfürstlichen Hoch und Schwartz Waldungen.*

Frelich, L.E. and Lorimer, C.G. 1985 Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. *Biol. Conserv.* **34**, 99–120.

Gaspersic, F. 1967 Razvojna dinamika mesanih gozdov jelke-bukve na Snezniku v zadnjih sto letih (in Slovene). *Gozdarski vestnik.* **25**, 202–237.

Gill, R.M.A. 1992 A review of damage by mammals in north temperate forests. 3. Impact on trees and forests. *Forestry.* **65**, 363–388.

Heuze, P., Schnitzler, A. and Klein, F. 2005 Consequences of increased deer browsing winter on silver fir and spruce regeneration in the Southern Vosges mountains: implications for forest management. *Ann. For. Sci.* **62**, 175–181.

Jerina, K. 2008 *Velika rastlinojeda divjad in razvojna dinamika gozdnih ekosistemov: proucevanje vplivov izbranih okoljskih in populacijskih parametrov ter gozdno-gojitvenih sistemov na zmoznosti naravne obnove: Research Report (in Slovene).* Biotechnical faculty, Department for Forestry and Renewable Forest Resources, Ljubljana, Slovenia.

Johann, E. 2007 Traditional forest management under the influence of science and industry: the story of the alpine cultural landscapes. *For. Ecol. Manage.* **249**, 54–62.

Klopcic, M., Jerina, K. and 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.

Kordis, F. 1993 *Dinaric Fir-Beech Forests in the Republic of Slovenia (in Slovene).* Biotechnical faculty, Department for Forestry and Renewable Forest Resources, Ljubljana, Slovenia.

Korpel, S. 1995 *Die Urwälder der Westkarpaten (in German).* Gustav Fisher Verlag, Stuttgart, Germany.

Kovac, M., Kusar, G., Hocevar, M., Simoncic, P., Poljanec, A., Skudnik, M. *et al.* 2009 *Control Sampling Method in Slovenia—History, Characteristics and Use (in Slovene).* Slovenian Forestry Institute, Silva Slovenica, Ljubljana, Slovenia.

Larsen, J.B. 1986 Silver fir decline—a new hypothesis concerning this complex decline syndrome in Abies alba (Mill). *Forstwiss. Centralbl.* **105**, 381–396.

Larsen, J.B. 1995 Ecological stability of forests and sustainable silviculture. *For. Ecol. Manage.* **73**, 85–96.

Leak, W.B. and Filip, S.M. 1977 Thirty-eight years of group selection in New England Northern Hardwoods. *J. For.* **75**, 641–643.

Lexerød, N.L. and Eid, T. 2006 An evaluation of different diameter diversity indices based on criteria related to forest management planning. *For. Ecol. Manage.* **222**, 17–28.

Linder, P. 1998 Structural changes in two virgin boreal forest stands in central Sweden over 72 years. *Scand. J. For. Res.* **13**, 451–461.

Linder, P. and Östlund, L. 1998 Structural changes in three mid-boreal Swedish forest landscapes, 1885–1996. *Biol. Conserv.* **85**, 9–19.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J. *et al.* 2010 Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *For. Ecol. Manage.* **259**, 698–709.

Minami, M. 2000 *Using ArcMap. GIS by ESRI.* Environmental Systems Research Institute, Inc., New York.

Montes, F., Sánchez, M. and Río Md, C.I. 2005 Using historic management records to characterize the effects of management on the structural diversity of forests. *For. Ecol. Manage.* **207**, 279–293.

Moore, P.D., Webb, J.A. and Collinson, M.E. 1997 *Pollen Analysis.* 2nd edition. Blackwell, London.

Motta, R. and Garbarino, F. 2003 Stand history and its consequences for the present and future dynamic in two silver fir (Abies alba Mill.) stands in the high Pesio Valley (Piedmont, Italy). *Ann. For. Sci.* **60**, 361–370.

Nagel, T., Svoboda, M., Rugani, T. and Diaci, J. 2010 Gap regeneration and replacement patterns in an old-growth Fagus–Abies forest of Bosnia–Herzegovina. *Plant Ecol.* **208**, 307–318.

O'Hara, K.L., Hasenauer, H. and Kindermann, G. 2007 Sustainability in multi-aged stands: an analysis of long-term plenter systems. *Forestry.* **80**, 163–181.

Oliver, C.D. and Larsen, B.C. 1996 *Forest Stand Dynamics.* Wiley, New York.

Patil, G.P. and Taillie, C. 1982 Diversity as a concept and its measurement. *J. Am. Stat. Assoc.* **77**, 548–561.

Pickett, S.T. and White, P.S. 1985 *The Ecology of Natural Disturbance and Patch Dynamics.* Academic Press, San Diego, CA.

Prpic, B. (ed.) 2001 *Silver fir in Croatia.* Hrvatske sume p.o, Zagreb: Akademija sumarskih znanosti. Zagreb, Croatia.

Schuster, W.S.F., Griffin, K.L., Roth, H., Turnbull, M.H., Whitehead, D. and Tissue, D.T. 2008 Changes in composition, structure and aboveground biomass over seventy-six years (1930–2006) in the Black Rock Forest, Hudson Highlands, southeastern New York State. *Tree Physiol.* **28**, 537–549.

Schweingruber, F.H. 1996 *Tree Rings and Environment. Dendroecology.* Bern, Switzerland, Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf, Paul Haupt Verlag.

Sendak, P.E., Brissette, J.C. and Frank, R.M. 2003 Silviculture affects composition, growth, and, yield in mixed northern conifers: 40-year results from the Penobscot Experimental Forest. *Can. J. For. Res.* **33**, 2116–2128.

Senn, J. and Suter, W. 2003 Ungulate browsing on silver fir (Abies alba) in the Swiss Alps: beliefs in search of supporting data. *For. Ecol. Manage.* **181**, 151–164.

Sercelj, A. 1996 *The Origins and Development of Forests in Slovenia.* Slovenska akademija znanosti in umetnosti, Ljubljana, Slovenia.

Solomon, D.S. and Gove, J.H. 1999 Effects of uneven-age management intensity on structural diversity in two major forest types in New England. *For. Ecol. Manage.* **114**, 265–274.

Stancioiu, P.T. and O'Hara, K.L. 2006 Regeneration growth in different light environments of mixed species, multiaged, mountainous forests of Romania. *Eur. J. For. Res.* **125**, 151–162.

Swetnam, T.W., Allen, C.D. and Betancourt, J.L. 1999 Applied historical ecology: using the past to manage for the future. *Ecol. Appl.* **9**, 1189–1206.

van der Maarel, E. 2005 *Vegetation Ecology.* 1st edn. Blackwell, Malden, MA.

Veselic, Z. and Robic, D. 2001 *Posodobitev poimenovanja sintaksonov, ki nakazujejo (indicirajo) skupine rastisc, njihove podskupine in rastiscne tipe v racunalniski bazi CE ZGS: tipkopis (in Slovene).* Slovenia Forest Service, Ljubljana, Slovenia.

Vrska, T., Adam, D., Hort, L., Kolár, T. and Janík, D. 2009 European beech (Fagus sylvatica L.) and silver fir (Abies alba Mill.) rotation in the Carpathians—a developmental cycle or a linear trend induced by man? *For. Ecol. Manage.* **258**, 347–356.

Weiner, J. and Solbrig, O.T. 1984 The meaning and measurement of size hierarchies in plant populations. *Oecologia*. **61**, 334–336.

Wick, L. and Mohl, A. 2006 The mid-Holocene extinction of silver fir (Abies alba) in the Southern Alps: a consequence of forest fires? Palaeobotanical records and forest simulations. *Veg. His. Archaeobot.* **15**, 435–444.

Yoshida, T., Noguchi, M., Akibayashi, Y., Noda, M., Kadomatsu, M. and Sasa, K. 2006 Twenty years of community dynamics in a mixed conifer—broad-leaved forest under a selection system in northern Japan. *Can. J. For. Res.* **36**, 1363–1375.

Zar, J.H. 2010 *Biostatistical Analysis*. 5th edition. Pearson, Education International, Upper Saddle River, NJ.

Received 10 August 2010

2.2 LONG-TERM CHANGES OF STRUCTURE AND TREE SPECIES COMPOSITION IN DINARIC UNEVEN-AGED FORESTS: ARE RED DEER AN IMPORTANT FACTOR?

Klopčič M., Jerina K., Bončina K. 2010. Long-term changes of structure and tree species composition in Dinaric uneven-aged forests: are red deer an important factor? = [Spremembe zgradbe in drevesne sestave dinarskih raznomernih gozdov v dolgem časovnem obdobju: ali je jelenjad pomemben dejavnik?]. European Journal of Forest Research, 129, 3: 277-288

Eur J Forest Res (2010) 129:277–288
DOI 10.1007/s10342-009-0325-z

ORIGINAL PAPER

Long-term changes of structure and tree species composition in Dinaric uneven-aged forests: are red deer an important factor?

Matija Klopcic · Klemen Jerina · Andrej Boncina

Received: 11 March 2009 / Revised: 1 September 2009 / Accepted: 9 October 2009 / Published online: 19 November 2009

Abstract Uneven-aged silver fir-European beech forest stands were studied to (1) analyse the dynamics of diameter structure and tree species composition in the past two centuries and (2) determine the impact of red deer on the regeneration and recruitment of silver fir. The study used current data on forest stands, archival data from old forest management plans for the period 1789–2004, and red deer harvesting records for the period 1907–2006. During the observation period, the silver fir population aged and silver fir and European beech alternated in dominance. The study revealed a strong impact of red deer on the composition and recruitment of tree regeneration, especially on silver fir regeneration. The drastic changes in red deer density (from extermination up to 5.8 animals km^{-2}) and past forest management practices were apparently the main factors driving the population dynamics of silver fir (regeneration, recruitment, and diameter structure) in the study area during the past two centuries.

Keywords Uneven-aged forests · Stand dynamics · Archival data · Silver fir · Red deer · Browsing

Introduction

The composition and structure of forest stands are a result of the complex interplay between growth conditions, natural and anthropogenic disturbances (Oliver and Larsen 1996), and inter- and intra-specific relationships (van der Maarel 2005). Natural disturbance—an important driver of stand dynamics—may be one-off events such as windthrows, fires, avalanches, and floods, or continuous events such as the impact of ungulate browsing on tree species regeneration (Pickett and White 1985). One of the key anthropogenic disturbances is forest management, which has a profound impact on the structural and spatio-temporal dynamics of forest stands.

Over the last centuries in Europe, forest management has caused large-scale changes in the spatial distribution, tree species composition, and structure of forest stands (Johann 2007). In the eighteenth and nineteenth centuries, even-aged forestry created large areas of uniform, mainly conifer-dominated forest stands. On the other hand, the application of uneven-aged systems in the nineteenth and the twentieth centuries (Diaci 2006; Johann 2007) has maintained mixed, more structurally diverse, and heterogeneous forest stands. Uneven-aged forest stands are considered stable in terms of structure and composition (e.g. Larsen 1995).

Selection management (Schütz 2001) is a form of uneven-aged forest management and is characterised by continuous forest cover, negligible fluctuations in growing stock and tree species composition, and continuous natural regeneration. Selection forests are widespread, particularly in Switzerland, Germany, France, Italy, Slovenia, and Croatia; they are often mountainous forests of silver fir (*Abies alba* Mill.), European beech (*Fagus sylvatica* L.), and Norway spruce (*Picea abies* (L.) Karst.). Silver fir is frequently the key tree species, and without it, the maintenance of selection structures of forest stands is less successful (Korpel 1995; Schütz 2001). The most important conditions for the maintenance of a selection structure are

Communicated by C. Ammer.

M. Klopcic · K. Jerina · A. Boncina (✉)
Department of Forestry and Renewable Forest Resources,
Biotechnical Faculty, University of Ljubljana, Vecna pot 83,
1000 Ljubljana, Slovenia
e-mail: andrej.boncina@bf.uni-lj.si

ongoing regeneration and the recruitment of smaller-diameter trees into larger diameter classes. Silvicultural measures in particular have a profound impact on these conditions, but other factors may be important as well. For example, the selective browsing of large ungulates on regeneration and differences in how tree species recover from browsing co-determine the species composition of regeneration and reduce the recruitment of the most palatable tree species (Gill 1992b).

Due to the palatability and slow juvenile growth of silver fir, and consequently, the longer exposure to browsing, fir is one of the most susceptible European tree species to the impact of large herbivores. In some areas in Central Europe, such as in the Alps and in the Dinaric Mountains, silver fir regeneration may be browsed to the extent that it never passes the germination phase (Ott 1989; Motta 1996; Senn and Suter 2003; Jarni et al. 2004; Heuze et al. 2005). Many researchers emphasise that large herbivores have been a factor driving the profound changes in tree species composition of Central European forests since the beginning of the twentieth century (Gill 1992a; Ammer 1996; Putman 1996). The impact of browsing has varied as the population densities of large herbivores changed over space and time. A frequent obstacle to arriving at more reliable findings about the long-term impact of large herbivores on the development of forest stands has been a lack of research based on long-term datasets. Senn and Suter (2003) established that most existing research provides only indirect evidence of the impact of large herbivores on the long-term dynamics of forest stands and silver fir populations. Moreover, at the landscape level, there are very few studies of the long-term dynamics of selection forest stands in Central Europe (e.g. Gaspersic 1967; Boncina et al. 2003; O'Hara et al. 2007).

Long-term dynamics of forest stands are studied with a variety of methods: (1) palynological methods (e.g. Moore et al. 1997) make it possible to study tree species composition over several millennia; (2) dendrochronological methods (e.g. Schweingruber 1996; Swetnam et al. 1999) allow the reconstruction of the development of trees for periods spanning several centuries; and (3) archival data such as forest management plans, forest maps, land registers, felling records, and game harvesting records, which are a neglected source of information, make it possible to quantify long-term changes in forest structure and to better understand the impacts of a changing natural and anthropogenic disturbance regime over the past few decades or centuries (Axelsson et al. 2002; Chapman et al. 2006).

In Slovenia, regular forest management has a long and rich tradition (Boncina et al. 2003). Selection management, practised in 4% of Slovenian forests (Boncina et al. 2002), is well established in the Dinaric Mountains (Hufnagl 1893; Schollmayer 1906), an area that is home to a large, continuous complex of silver fir-European beech forests. These forests are a suitable object for the study of long-term changes of forest stands: detailed data on the structure and composition of forest stands and felled timber are available for a period spanning more than a century. The area is also suitable for studies of the impact of large herbivores on the development of forest stands: the population density of red deer (*Cervus elaphus* L.), the most widespread and ecologically the most significant species of large herbivore in the area (Jerina 2006), has changed dramatically over the past two centuries. Preserved archives of the annual harvest of red deer make it possible to estimate its population dynamics with sufficient accuracy. Additionally, the browsing of regeneration has been regularly monitored there for more than 30 years in both fenced and non-fenced areas. The aim of this study was thus (1) to study changes in diameter structure and tree species composition of uneven-aged selection silver fir-European beech forests over the last two centuries and (2) to determine the impact of red deer on regeneration and changes in diameter structure of silver fir.

Methods

Study area

The Dinaric Mountains stretch from Slovenia through Croatia and Bosnia and Herzegovina to Montenegro and Albania. The Dinaric silver fir-European beech (hereafter fir-beech) forests form one of the largest forest areas in Central Europe; in Slovenia, these forests represent 14% of the total forest area (Boncina et al. 2002). There is a long tradition of forest and wildlife management in these forests; the first forest management plans were made in the eighteenth century. A concept of nature-based forestry with single-tree and group selection as the prevalent silvicultural systems has been used from the beginning of the twentieth century, when adaptive forest management similar to Biolley's concept in Switzerland began (Hufnagl 1893; Schollmayer 1906). Earlier, in the eighteenth and nineteenth centuries, exploitation involved mainly broadleaves, which were used for the production of charcoal and potash; the intensity of exploitation peaked in the second half of the nineteenth century (Perko 2002).

The dynamics of forest stands were studied in the forest management unit (FMU) Leskova dolina (Fig. 1), which is located in southern Slovenia (45°36′N; 14°28′E) and comprises 2,456 ha of uneven-aged fir-beech forests divided into 131 compartments. Elevation ranges between 740 and 1,350 m above sea level. The area has abundant precipitation (2,166 mm year^{-1}), which is evenly distributed through the year. The average annual temperature is 6.5°C,

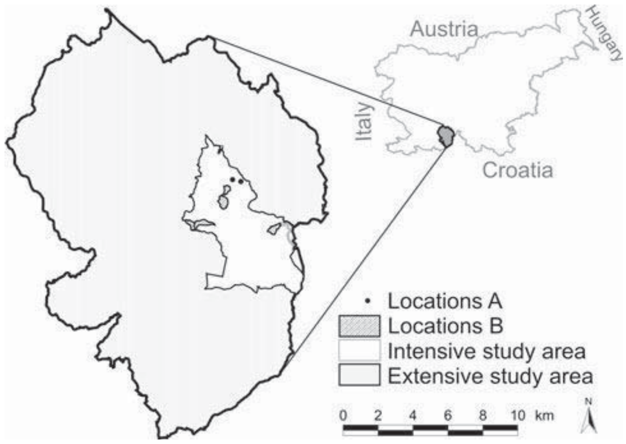

Fig. 1 Intensive (2,456 ha) and extensive (approx. 18,000 ha) study area of FMU Leskova dolina with locations of fenced areas (*locations A*) and compartments where ages of mature silver firs were determined (*locations B*)

with a mean monthly maximum temperature of 16.4°C in July and a mean minimum of −3.4°C in January. Late spring and early autumn frosts are common, and the snow cover duration averages 90 days (122 days maximum); the area is often not snow-free until late spring. The bedrock is carbonate, mainly limestone and some dolomite. Eutric cambisols of various depths developed on this bedrock, and in some parts, there are rendzinas of various depths. Fir is the dominant species, accounting for 50% of the total growing stock, followed by beech (26%), spruce (18%), and sycamore (*Acer pseudoplatanus* L.) with 2%. Other tree species (elm *Ulmus glabra* L., small-leaved lime *Tilia cordata* Mill., rowan *Sorbus aucuparia* L., and yew *Taxus baccata* L.) altogether account for less than 4% of the total growing stock. The average growing stock is 428 m^3 ha^{-1}, and the annual increment is 9.3 m^3 ha^{-1} (FMP 2004). Forest stands in every compartment have undergone selection cutting approximately once per decade with an average cutting intensity of 6.9 m^3 ha^{-1}.

The study area is home to three species of large herbivores: red deer, roe deer (*Capreolus capreolus* L.), and chamois (*Rupicapra rupicapra* L.). The forest cover of the area is high (94%), and there are few pastures, which makes for considerable browsing pressure on forest vegetation (Jerina 2008). In the extensive study area (Fig. 1), red deer density is relatively high (about 3 animals km^{-2}; this study), whereas the density of roe deer (1.3 km^{-2}) and chamois (0.04 km^{-2}) is low (Jerina unpublished). However, in spatial terms, ungulate densities in the extensive study area are heterogeneous: roe deer density is the highest at the foot of the hills, where the forest cover is lower; chamois is found only on peaks in the southern section of the extensive study area; and red deer are the dominant species in the intermediate zone, where fir-beech forests abound. This intermediate fir-beech zone is also where the tree regeneration sampling plots were located in our study. For most of the Holocene up to the March revolution in 1848, red deer was probably a common species (Fabjan 1956; Adamic 1992; Jerina 2006). After 1848, it disappeared due to over-harvesting, and in 1907, it was reintroduced (Adamic 1992). Its density did not start growing rapidly again until after World War II, reaching a maximum in 1976 (5.8 km^{-2}), whereupon it halved in just a few years as intense shooting was mandated to reduce browsing damage to forests; since then, red deer density has fluctuated around this value (2005: 3 km^{-2}) (Jerina 2006; this study).

Archival data acquisition and database creation

The dynamics of forest stands in the period 1789–2004 were studied on the basis of archival data acquired from the land register and old forest management plans kept in the Archives of the Republic of Slovenia and at the Slovenia Forest Service (Table 1). The oldest data on forests in the FMU Leskova dolina were acquired from the Josephinian land register of 1789. Detailed analysis was carried out on data from eight preserved forest management plans (FMP) for the study area, which were made in 1864, 1912, 1936, 1954, 1964, 1974, 1994, and 2004. The plans include the results of forest inventories at the level of compartments ($N = 131$; average compartment size = 18.75 ha). The intra-compartment boundaries hardly changed between 1864 and 2004, but the methods of forest inventories did. In 1789 and 1864, ocular assessments of the tree species composition of compartments were made. Most subsequent inventories involved full callipering of forest compartments (FMP 1912, 1936, 1954, 1964, 1974). All trees above a diameter at breast height (dbh) of 8 cm (FMP

Table 1 Sources of data

Source keeper	Source	Year of source
Archives of the Republic of Slovenia	Josephinian land register	1789
Slovenia forest service	Forest management plan (FMP) for forest management unit Leskova dolina	1864, 1912, 1936, 1954, 1964, 1974, 1994, 2004
	Database on permanent sampling plots	2008

1912), 10 cm (FMP 1954, 1964, 1974) or 12 cm (FMP 1936) were measured. The number of measured trees was high (e.g. 1,339,611 trees were measured in 1954). In the last two decades, the inventory of forest stands was carried out on permanent sampling plots (grid 200 × 250 m; area = 500 m^2; $N = 486$), where trees ≥10 cm in dbh were measured.

The structure of the forest stand data is not entirely consistent. Typically, the inventory of a forest compartment includes information on the dbh structure (number of trees per dbh class and tree species), tree species composition (share of individual tree species in total growing stock), growing stock (m^3 ha^{-1}), and annual increment (m^3 ha^{-1}); data for 1789 and 1864 are an exception because they include only assessments of tree species composition in forest stands. In the 1912 and 1936 inventory, data on the dbh structure of forest stands by compartment are not shown for individual species but only aggregated for broadleaves and conifers. Inventory data on the number of trees are provided in non-consistent diameter classes. For 1912 and 1936, the trees were classified into 10-cm dbh classes (FMP 1912, 1936) and for all other years in 5-cm dbh classes (FMP 1954, 1964, 1974, 1994, 2004); data were therefore combined and shown on a single scale—in 10-cm dbh classes. The growing stock of individual forest tree species and forest stands was calculated with Biolley tariffs. Additional useful information was acquired from the text in the FMPs.

Analysis of age of mature silver fir trees

To examine the age and period of unsuppressed growth of mature fir trees in the area covered by this study, 221 mature fir trees (dbh ≥ 40 cm) in five randomly chosen compartments (Fig. 1) were analysed; this analysis was done in the field on freshly cut stumps.

Reconstruction of population dynamics of red deer

The population dynamics of red deer were reconstructed on the basis of data on harvest and loss (found dead animals, roadkill etc.), which were collected for the 1907–1938 period by Fabjan (1956); after 1948, these data were gathered systematically according to law in the official hunting registers. The quality of the available data changed over time: after 1976, data on the sex and age of extracted animals have been gathered, but previously only the data on total annual harvest were collected; during and for a short period after World War I (1914–1918) and World War II (1940–1946), hunting statistics were not kept. Accordingly, the dynamics of the population density were reconstructed with multiple methods: (1) for the period after 1976, with the "population reconstruction" method (see Roseberry and Woolf 1991); this method is based on the number and age of harvested animals, which are then used to reconstruct the number of animals that lived in a specific year. For example, for year X, records show the harvest of N animals aged 0+, in year $X + 1$, M number of animals aged 1+, in year $X + 2$, P number of animals aged 2+, etc. In year X, the number of animals aged 0+ was thus $N + M + P +$ etc.; the same method is used to calculate the number of animals aged 1+, 2+, etc. for the individual years and the number of all animals in a given year; (2) for the period 1907–1976, the densities were reconstructed with a multivariate linear regression model which was build based on the data for 1976–2007 (in the model estimated, red deer density is the dependent variable and red deer harvest data are the independent variables); the model forecasts density in year X on the basis of a known number of extractions in year X and several years thereafter; and (3) for the years 1914–1918 and 1940–1946, the numbers were reconstructed with linear interpolation of density values before and after this period.

Browsing on regeneration

To determine the impact of red deer on the composition of the regeneration (dbh < 10 cm), the regeneration in two fenced (one 19 ha and one 2 ha; locations in Fig. 1) and two non-fenced areas was analysed in 2008. The fences were built 35 years ago and have been under permanent control by local professional foresters since then. Stand conditions are similar within and outside the fenced areas: they are dominated by stands with small canopy gaps and a growing stock of about 450 m^3 ha^{-1}. A total of 66 plots of 16 m^2 were surveyed, which included 33 plots within both fenced areas and 33 outside the fenced areas; the approach (size and number of plots) was adopted by Boncina (2000) and Jarni et al. (2004). The location of the first randomly selected plot within each fenced area defined the origin of the transect that ran parallel to the fence. Plots were placed at 4-m intervals along the transects. Transects outside the fenced areas were parallel to the ones inside and placed at a similar distance from the fence as the transects inside (approximately 50 m from a fence). On each plot, seedlings ($h < 130$ cm) and saplings ($h \geq 130$ cm and dbh < 10 cm) were recorded for each tree species and classified by height class (<20 cm; 20–49 cm; 50–89 cm; 90–129 cm; ≥130 cm and dbh < 10 cm). Additionally, browsing damage of the terminal shoot of each tree was recorded. The differences in the number of seedlings and saplings by tree species between fenced and non-fenced areas were examined using the non-parametric Mann–Whitney U test, since not all of the data were distributed normally (Hollander and Wolfe 1999).

Browsing of fir seedlings for the period 1977–2004 was analysed on the extensive area of FMU Leskova dolina (Fig. 1) based on records from permanent sampling plots. Eight consecutive seedling inventories in 1977, 1981, 1983, 1985, 1987, 1989, 1992, and 1994 were carried out on 147 sampling plots, while three consecutive inventories (1996, 2000, 2004) were carried out on 64 sampling plots (e.g. Veselic 1991; Jerina 2008). On 5 × 5 m plots, all seedlings were tallied by tree species and height class (<15 cm; 15–29 cm; 30–129 cm) and recorded as browsed or unbrowsed. Only summary data (for all plots combined) are available for the first inventory. Consequently, the analysis always considered summary data for individual years. Because variation in red deer density may potentially affect both browsing intensity and fir seedling density, both indicators were analysed. A correlation between browsing intensity and red deer density, and seedling density and red deer density was estimated with the non-parametric Kendall's tau-b correlation analysis; its advantage is in the sensitivity to all monotonous and not just linear correlations between variables, and it does not presume a normal distribution of variables (Hollander and Wolfe 1999).

Results

Long-term forest stand dynamics

The tree species composition of uneven-aged fir-beech forests in the FMU Leskova dolina underwent profound change during the 1789–2004 period (Table 2). At the end of the eighteenth century, broadleaves accounted for the bulk of the growing stock (76%). Conifers made up 24% of the growing stock and were dominated by fir; few spruce trees were present. By the middle of the nineteenth century, the composition of the forest stands changed substantially: the share of conifers, particularly fir, rose and the share of beech and other broadleaves fell. This trend continued until 1974, when conifers reached the highest share of the growing stock (80%) and fir accounted for as much as two-thirds of the total growing stock. After 1974, the share of broadleaves, especially beech, increased notably, and the share of conifers dropped. Among the conifers, the share of fir in total growing stock dropped from 68 to 50% by 2004. Spruce was very rare in the stands in 1912, whereupon its share of the total growing stock rose continually, doubling between 1954 and 2004.

At the beginning of the twentieth century, the growing stock of the forest stands was low (234 m^3 ha^{-1}) due to heavy exploitation at the end of the nineteenth century. After 1912, the total growing stock increased, by as much as 83% by 2004.

Data on tree species composition and total growing stock of the forest stands indicate an ageing of the stands and an alternation between fir and beech; this has been additionally confirmed by an analysis of the dbh structure of the forest stands. In the period 1912–2004, the dbh structure of the forest stands maintained a reversed *J*-shaped distribution (Fig. 2a). However, significant changes are evident: the number of medium-sized (dbh = 30–49 cm) and large-sized (dbh ≥ 50 cm) trees increased and the number of small-sized trees (dbh = 10–29 cm) dropped constantly.

The largest changes occurred in the dbh structure of fir (Fig. 2b). In 1912, there were hardly any firs equal to or more than 50 cm in dbh (4 ha^{-1}), but their number grew to 20 trees per ha by 1954, and in 2004, there were 36 large-sized diameter firs per ha. Between 1912 and 2004, the number of small-sized diameter firs (dbh = 10–19 cm) dropped drastically from 190 to 30 ha^{-1}, respectively. The results suggest a successive ageing of the fir population coupled with insufficient recruitment of young firs to the stand canopy (see also Fig. 3b).

Half of the current generation of mature firs (dbh ≥ 40 cm) germinated in a relatively short period between 1829 and 1846 (Table 3). The period of unsuppressed growth of the studied firs started at the end of the nineteenth century.

Table 2 Development of tree species composition (% of growing stock) and growing stock (m^3 ha^{-1}) of forest stands, 1789–2004

	Year								
	1789	1864	1912	1936	1954	1964	1974	1994	2004
Tree species composition									
Conifers	24	49	70	80	77	76	80	71	67
Silver fir	*	*	*	*	68	65	68	55	50
Norway spruce	*	*	*	*	9	11	12	16	18
Broadleaves	76	51	30	20	23	24	20	29	33
European beech	*	*	*	*	17	20	16	24	26
Other species	*	*	*	*	5	4	4	6	7
Growing stock	*	*	234	308	354	374	340	402	428

* No data available

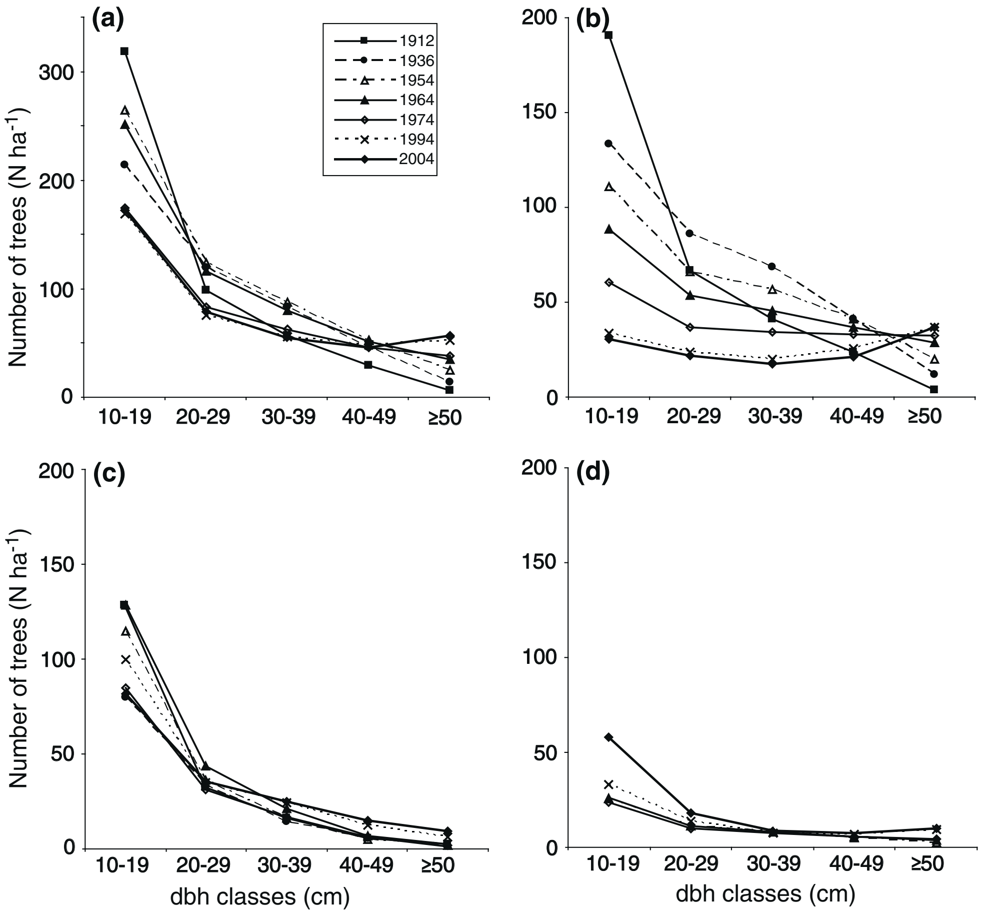

Fig. 2 Diameter structure dynamics of forest stands **a** and populations of individual tree species, **b** silver fir, **c** European beech, and **d** Norway spruce

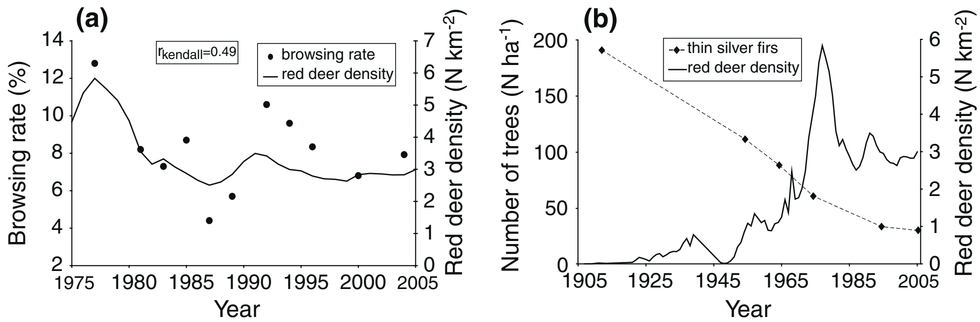

Fig. 3 **a** Correlation between red deer density and browsing of silver fir seedlings, 1977–2004; **b** comparison of red deer density in the period 1900–2006 and number of small-sized diameter silver firs (dbh = 10–19 cm) in studied forest stands

Table 3 Mean year of germination and start of unsuppressed growth of mature silver firs (dbh ≥ 40 cm) including the lower and upper quartile boundaries

	Mean	Lower quartile (25%)	Upper quartile (75%)
Year of germination	1838	1829	1846
Beginning of unsuppressed growth	1885	1875	1897

The dbh structure of beech in the period 1912–2004 (Fig. 2c) did not indicate such significant changes as that of fir; in the last two decades, the number of large- and medium-sized diameter beeches increased substantially, resulting in a notable increase in its share in the total growing stock (Table 2). The dbh structure of spruce (Fig. 2d), meanwhile, shows a gradual increase in the number of smaller-sized diameter trees in the period 1974–2004, indicating that spruce is being recruited into the stands.

The impact of red deer on regeneration, recruitment, and diameter distribution dynamics of silver fir

Analysis of browsing on regeneration in fenced and non-fenced areas in 2008 showed that selective browsing by large herbivores had a major impact on the density and species composition of the regeneration. No statistically significant differences were found between the fenced and non-fenced areas for total regeneration density ($P = 0.078$), but there were statistically significant differences in the density of seedlings and saplings in some height classes (Table 4). Statistically significant differences between the two areas were also found for the density of fir regeneration ($P = 0.000$); in the fenced areas, the density of fir regeneration was 4.8 times higher than in the non-fenced areas. The differences are even more obvious by height classes: no statistically significant differences were found for the density of fir seedlings up to 20 cm in height, but in the 20- to 49-cm class, there were 50 times more fir seedlings in fenced areas; no fir seedlings higher than 50 cm or fir saplings were registered in non-fenced areas. Similar results were found for sycamore: in fenced areas, the number of sycamore seedlings up to 20 cm high and seedlings in the 20- to 49-cm class was significantly lower than in non-fenced areas ($P = 0.000$ and $P = 0.000$, respectively), but the recruitment of sycamore seedlings into higher classes was noticeably higher in the fenced areas. The density of beech regeneration was higher in non-fenced than in fenced areas, but the difference was not statistically significant ($P = 0.087$). Spruce was hardly registered at all in the regeneration layer.

In the years when records of seedling ($h < 130$ cm) browsing in the extensive area of FMU Leskova dolina were made (1977–2004), the red deer density changed significantly (Fig. 3a). The highest density was recorded in 1977 (5.8 km^{-2}) and the lowest 10 years later, in 1987 (2.5 km^{-2}). The density and browsing of fir seedlings are strongly related to their height. The average density of all fir seedlings in one inventory in 1977–2004 was nearly 24,000 individuals ha^{-1}, the browse rate (the rate of browsed individuals among all individuals) was 8.2%, and fir's share of total seedlings (the share of seedlings of one tree species in the total number of seedlings) was over 25%. The average density of fir seedlings over 15 cm was 314 individuals ha^{-1}, the browse rate exceeded 38%, and the share of fir in the seedlings of the same height category dropped to 1.6%. Finally, only an average of 44 firs ha^{-1} was registered in the highest class (30–129 cm), of which 71% on average were browsed, and the share of fir in total seedlings above 30 cm dropped to only 0.6%. In 4 of the 11 monitoring years, all firs above 30 cm were browsed; in one census (in 1994), there were no firs over 30 cm at all. The signs of correlations (Table 5) between the density and browsing intensity of fir seedlings and red deer density were mostly in accordance with expectations, but only the correlation between the browsing rate to all fir seedlings and red deer density was statistically significant ($r = 0.49$; $P = 0.036$; $n = 11$).

Recruitment of fir into small-diameter trees dropped constantly over the studied period (Fig. 3b). The number of small-sized diameter firs (dbh = 10–19 cm) in the forest stands was significantly higher in 1912 than in 1954 or 2004, at 190, 111, and 30 trees, respectively. A similar trend was evident in the share of fir in the total number of small-sized diameter trees (results not shown); both started to drop before the red deer density began to rapidly increase.

Table 5 Kendall's tau-b correlation coefficient (*r*; *P*-values are also shown) between density of silver fir by height classes and red deer density, and between browsing rate of silver fir seedlings by height classes and red deer density, 1977–2004

	Silver fir seedlings					
	>15 cm in height		>30 cm in height		Total	
	r	*P*	*r*	*P*	*r*	*P*
Density of fir	−0.11	0.655	0.22	0.369	−0.13	0.586
Browsing rate of fir	0.02	0.929	−0.12	0.661	0.49	0.036

Table 4 Mean density of seedlings and saplings (N ha^{-1}) of different tree species by height classes in non-fenced (N_{NF}) and fenced (N_F) areas and comparison of densities between non-fenced and fenced areas (Mann–Whitney *U* test; *P*-values are shown)

Height class (cm)	Silver fir			European beech			Sycamore			All species		
	N_{NF}	N_F	*P*	N_{NF}	N_F	*P*	N_{NF}	N_F	*P*	N_{NF}	N_F	*P*
<20 cm	3,352	6,042	0.520	6,553	1,761	0.002	9,773	1,420	0.000	20,625	9,451	0.002
20–49 cm	152	4,962	0.000	10,417	4,337	0.002	7,481	1,383	0.000	19,981	11,117	0.007
50–89 cm	0	1,648	0.000	6,023	3,958	0.216	966	1,042	0.260	7,405	6,894	0.520
90–129 cm	0	549	0.000	3,011	2,992	0.831	38	511	0.000	3,068	4,261	0.069
≥130 cm	0	625	0.001	3,693	5,720	0.016	0	777	0.000	3,712	7,898	0.000
Total	3,504	13,826	0.000	29,697	18,769	0.087	18,258	5,133	0.003	54,792	39,678	0.078

Discussion

Archival data enables detailed reconstructions of the development of forest stands and the factors that affect this development (Axelsson et al. 2002; Chapman et al. 2006). However, cautious analysis is indispensable when data from different archive sources are used, because differences between data sets are easily confused with structural changes of forest stands (Radeloff et al. 1999; Agnoletti and Anderson 2000). Archival data describe the state of forest stands at a certain point in time. This is just one of many—albeit perhaps noteworthy different—states in time over the long-term development of forest stands, a fact which needs to be considered in the interpretation of the results. However, with a large enough density of such points (which archival data enable), it is possible to clearly describe the dynamics of forest stands over a long period.

In terms of the data quality on stand parameters and the length of the period the data cover, this study area is one of the best in Slovenia, and the data are of similar quality as in other similar studies (e.g. Linder and Östlund 1998; Axelsson et al. 2002; Montes et al. 2005). Nevertheless, some problems appeared in the acquisition of data and the preparation of the database on the stand parameters: in some inventories, the data were incomplete; the tree species composition was provided by groups of tree species; different inventory methods were used; and the dbh structures of the stands were provided in variously broad dbh classes.

We only examined the influence of red deer on regeneration, although roe deer and chamois also live in the study area. In the extensive study area, population densities, and in particular, biomass (as better indicator of ecological impacts) of roe deer and chamois are very low per se, especially when compared to red deer. The maximum biomass of red deer in the period 1976–2005 was 381 kg km^{-2}, whereas that of roe deer and chamois was 37 and 1.7 kg km^{-2}, respectively (Jerina unpublished). Moreover, the spatial distribution of the three ungulate species in the study area is very spatially heterogeneous: roe deer live mostly in the lowest-lying, less-forested areas; chamois at the highest altitudes; while the intermediate zone, where the sampling plots were located, provides ideal conditions for red deer. Consequently, the density and biomass estimation were underestimated for red deer and overestimated for roe deer and chamois. As a result, estimates of roe deer and chamois density dynamics would likely be too imprecise for use in the analysis of regeneration browsing.

The methods used to reconstruct the red deer density presume that all mortality was registered, but this is never entirely true. However, the reintroduction of red deer to the study area in 1907 was the first successful reintroduction of the species in the wider region (Adamic 1992) and therefore the subject of considerable and constant attention among both resource managers and hunters. Consequently, the data were gathered very meticulously, and there was no poaching because the area was managed by professional hunters. Additionally, due to problems with forest regeneration, foresters have been continuously pushing hunters to reduce the red deer density. Under Slovenian legislation, registered non-hunting mortality is considered as part of the total annual harvest. Because hunters did not agree with a strong reduction in red deer density, they were motivated to record non-hunting mortalities. In the study area, non-hunting mortality occurs mainly due to large predators [grey wolf (*Canis lupus* L.) and Eurasian lynx (*Lynx lynx* L.)], and only a portion of this mortality is registered (e.g. Smith et al. 2004; Krofel et al. 2008; Webb et al. 2008). But even if this fact was taken into account, the total estimated population size would not be significantly affected, as large predator-caused mortality represents a very low share of the total harvest (<10%) (Jerina unpublished). Furthermore, the study area is located in a forested mountain massif which is surrounded on most sides with non-forest areas, which makes the red deer population demographically very isolated. All the aforementioned factors are important because our methods assume no (or equalized) emigration and immigration and a 100% detection of dead animals (Roseberry and Woolf 1991). The calculated population densities were thus slightly, but constantly underestimated.

The population density of red deer fluctuated greatly during the study period, and therefore the minor errors in the red deer data should not decrease the ability to detect the impact of red deer on vegetation change. Furthermore, we were only concerned with the relative dynamics of the population parameters rather than absolute values. Therefore, we believe our data were appropriate for examining the research objectives.

Changes in composition and structure are a fundamental part of the natural dynamics of forest stands (Pickett and White 1985; Oliver and Larsen 1996). Management and other anthropogenic influences can only mitigate or intensify them. A comparison of studies based on archival data (e.g. Linder and Östlund 1998; Radeloff et al. 1999; Axelsson et al. 2002; Duchesne et al. 2005; Chapman et al. 2006; O'Hara et al. 2007; Vrska et al. 2009) reveals a variety of forest stand dynamics in different forest types and a wealth of leading impact factors, but a frequent common characteristic is the fluctuation in tree species composition and dbh structure. The traditional view is that composition and structure of selection forests do not alter substantially over a long period of time, yet this study concluded the opposite: during the 215-year observation period of fir-beech forest dynamics, the stand parameters changed a considerable degree.

Substantial changes in growing stock and dbh structure of forest stands were established in the observed period. The total growing stock of the stands increased as a result of a deliberate accumulation of volume increment (FMP 1912, 1954). Consequently, the number of large-sized diameter trees in the dbh structure of the forest stands rose. Boncina et al. (2003) found similar changes in other uneven-aged fir-beech forests in Slovenia. Those changes were the result of the first intensive forest exploitation at the end of the nineteenth century, which reduced the growing stock of forest stands, and the subsequent deliberate increase in growing stock of uneven-aged stands towards target values of about 400 m^3 ha^{-1} (FMP 1954; Gaspersic 1967). Similar changes were observed in Croatian Dinaric fir-beech forests (Cavlovic 2000), and analogous, albeit somewhat smaller, changes occurred also in Swiss plenter spruce-fir-beech stands in past 6–9 decades (O'Hara et al. 2007); this indicates similar dynamics of uneven-aged forests in Slovenia, Croatia, and Switzerland, and probably Central Europe in general.

The tree species composition of the studied forest stands changed drastically between 1789 and 2004. Fir underwent the greatest change, as its share of the total growing stock grew strongly at first, but then dropped in the final decades, from 68% in 1974 to 50% in 2004. At the same time, the share of beech and spruce in the total growing stock increased. Their dbh structures indicate a continued increase of their share in the forest stands over the coming decades. These findings correspond to the process of the alternation of dominant tree species (e.g. Simak 1951; Rabotnov 1992; Korpel 1995), yet our data suggest that this alternation is more a result of anthropogenic influences rather than a natural endogenous process; similar was found in the research in fir-beech forests of the Carpathians (Vrska et al. 2009). Furthermore, the study period is too short to reach a definite conclusion about fir-beech alternation with certainty. Nevertheless, fir has been reported to be frequently replaced by beech (e.g. Gaspersic 1974) and spruce (e.g. Heuze et al. 2005). Similar changes in the composition of fir-beech forests have also been documented in virgin forest remnants (e.g. Korpel 1995; Boncina 1999; Boncina et al. 2003; Diaci 2006), but the magnitude of changes was smaller than in our study area. The drop in the fir share in the growing stock of mixed forests and even a reduction in its distribution have been reported by researchers across Central Europe (e.g. Schütt et al. 1999; Senn and Suter 2003; Ficko and Boncina 2006).

Insufficient recruitment of fir into the stand canopy is the main impediment for the practice of selection forest management in the study area. This problem has been reported in many Central European countries (e.g. Motta 1996; Senn and Suter 2003; Heuze et al. 2005; Cavlovic et al. 2006). Of the factors that affect fir regeneration and recruitment in the study area, two factors stand out, both of them directly or indirectly triggered by man: (1) forest management and (2) ungulate browsing on regeneration.

From the middle of the nineteenth century to the middle of the twentieth century—a period of functionally negligible ungulate population densities—forest management was the main impact factor in the dynamics of the studied forest stands. Fir was present in the study area before the period covered by this study (Sercelj 1996) but the mature firs growing today germinated in the first half of the nineteenth century. The first major exploitation of these forests, in the second half of the nineteenth century, considerably reduced the growing stock of the stands and increased the light influx into the stands, which is reflected in the released growth of fir regeneration. In line with the economic principles of that time, foresters promoted conifers, in particular fir, in regeneration and among trees by weeding out beech (Perko 2002). At the beginning of the twentieth century, plenter management was introduced, but owing to the stands' origin, they did not have an entirely satisfactory plenter structure (Schollmayer 1906); by removing beech, foresters continued to promote conifers. The bulk of medium-sized diameter trees—mostly fir—in the growing stock of the forest stands and the planned accumulation of volume increment (Perko 2002) slowed down regeneration and recruitment of small-sized diameter trees into the stand canopy. In the first decades of the twentieth century, attempts were made to accelerate recruitment of fir by creating small gaps in stand canopy, but such conditions were more favourable for the regeneration and recruitment of broadleaves (Gaspersic 1967). The fact is that beech successfully germinated in stands dominated by fir, which regenerated abundantly in the mid-nineteenth century, when beech dominated the top layer. This strengthened a belief in the alternation of dominant tree species, ostensibly because of changes in soil conditions caused by tree litter (Gaspersic 1974; Pintaric 1978). In the period 1912–2004, the number of large-sized diameter trees, in particular fir, increased significantly, which indicates the ageing of forest stands and the fir population.

The ageing of fir-beech stands due to an insufficient regeneration and recruitment rate of fir has also been reported in Croatia (Cavlovic et al. 2006). A lack of regeneration and recruitment, and population ageing, has also been recorded for other species, including eastern hemlock (*Tsuga canadensis* (L.) Carr.) in mixed forests of Michigan, in the USA (Frelich and Lorimer 1985). A reduction in recruitment of small-sized diameter firs to the canopy of the analysed forest stands was recorded already in the period of low red deer density ($\leq$0.1 km^{-2}) at the beginning of the twentieth century. This suggests that some additional factors other than red deer browsing also affect fir recruitment, such as the structure and composition of forest stand, the density of the stand canopy, alelopathic relation between tree species, etc. (e.g. Gaspersic 1967; Pintaric 1978; Prpic et al. 2001).

The impact of large herbivores on forest stand dynamics varied significantly over time. After 1848, when the March revolution changed social relations and legal conditions also regarding hunting rights, red deer was completely exterminated (Fabjan 1956; Adamic 1992), which had a favourable effect on fir regeneration. The first exploitation of the studied forest stands, at the end of the nineteenth century, increased the food supply of shrubs, herbs, and grasses. Consequently, roe deer, which had then been present at very low densities, apparently did not have any noteworthy impact on tree regeneration, including the most sensitive species such as fir. In 1907, red deer was reintroduced to the study area, and after 1950, through a combination of favouring red deer in wildlife management, a low harvesting rate, and an absence of large predators, the population density started growing exponentially. The impact of red deer on vegetation, including tree seedlings, increased dramatically. In the 1980s and 1990s, browsing pressure was singled out by the forest service as the main problem of forest management in this area. After 1976, culling reduced the red deer population from 5.8 to about 3 km^{-2}, but the browsing rate was still high and recruitment into the stand canopy weak (Veselic 1991); obviously the great change in red deer density did not reduce damage to fir seedlings, although a drop in damage to sycamore and beech, for example, was registered (Debeljak et al. 1999).

Like elsewhere in mountainous mixed forests (e.g. Ott 1989; Motta 1996; Senn and Suter 2003; Heuze et al. 2005), in fir-beech forests, fir is one of the most susceptible species to browsing. The question that arises is at what densities of ungulates can fir still be successfully recruited into the stand canopy. A Slovenia-wide study (Jerina 2008) showed that relationships between large herbivore density and degree of fir browsing are explicitly non-linear and weak; a greater drop in the degree of browsing was recorded only for exceptionally low herbivore densities (e.g. red deer <1 km^{-2}), apart from that the intensity of fir browsing was constantly high. Present-day ungulate densities in the study area are generally not high (see Ammer 1996; Motta 1996; Heuze et al. 2005). However, the regeneration in fenced and non-fenced areas undeniably shows that red deer has a fundamental impact on regeneration and recruitment of fir and certain other tree species. The impact is even greater because the food capacity of the area is meagre due to a high forest cover (94%), high growing stock, and dense canopy.

Other factors may also be important for tree seedling recruitment and, consequently, changes in tree species composition, such as growing conditions, inter- and intra-specific relationships, general food availability in the forest stands, resistance of individual species to browsing, silver fir dieback, and climate change. (Gill 1992a, b; Debeljak et al. 1999; Petit and Lambin 2002; Bigler et al. 2004; van der Maarel 2005). Although these factors are complexly inter-related, they were not analysed in this study as it was presumed that they have a small impact compared to the studied factors. Some observations showed that on some sites with similar ungulate densities as in the study area, fir regenerates well (Jerina 2008), which means that the "target" density of ungulates that allows fir to regenerate and recruit to stand canopy varies depending on the other impact factors, among which inter- and intra-specific competition in combination with site and stand (light) conditions may play an important role. Just as Frelich and Lorimer (1985) found for eastern hemlock (*Tsuga canadensis* (L.) Carr.) in Michigan, USA, and Linder (1998) for Scots pine (*Pinus sylvestris* L.) and Norway spruce in Sweden, it is possible that fir needs a "window of opportunity" for successful recruitment into the stand canopy (Senn and Suter 2003)—a co-occurrence of appropriate conditions, including a low population density of large herbivores.

Forecasts of the future of fir in Dinaric fir-beech forests, and more broadly in Central Europe, are unreliable: this study and several others (e.g. Motta 1996; Heuze et al. 2005; Ficko and Boncina 2006; Jerina 2008) indicate that its share will continue to decline, probably to the level of the eighteenth century in our study area. The tree species composition before the analysed period cannot be completely determined; instead of hypothesizing a static ratio of tree species, it is more appropriate to understand it in the sense of "natural" fluctuations. Sercelj (1996) found that fir and beech have maintained a constant presence in fir-beech forests in Slovenia for the last 7,000 years, but, presumably due to changes in climate conditions, their relative dominance continuously changes. Anthropogenic impacts have mostly intensified these fluctuations, the extermination and reintroduction of red deer in the study area being such an example. Ungulate density (and its impact) likely went through changes before the period of our analysis as well, which may have contributed to past fluctuations in the tree species composition of forest stands.

Understanding the dynamics of the composition and structure of forest stands and the processes that drive these dynamics is an essential basis for present and future ecosystem-based forest management. Therefore, uneven-aged forest management should be more oriented towards managing the processes in forest ecosystems, and less towards maintaining static structures. Furthermore, uneven-aged forest management should not only be about stand management, since wildlife populations can have a strong influence on stand structure and composition.

References

Adamic M (1992) Red deer management (*Cervus elaphus* L.) in Republic Slovenia: the problems, recent trends and perspectives. Zbornik gozdarstva in lesarstva 39:47–60

Agnoletti M, Anderson S (eds) (2000) Methods and approaches in forest history. CABI Publishing, Wallingford

Ammer C (1996) Impact of ungulates on structure and dynamics of natural regeneration of mixed mountain forests in the Bavarian Alps. For Ecol Manag 88(1–2):43–53

Axelsson AL, Ostlund L, Hellberg E (2002) Changes in mixed deciduous forests of boreal Sweden 1866–1999 based on interpretation of historical records. Landscape Ecol 17(5):403–418

Bigler C, Gricar J, Bugmann H, Cufar K (2004) Growth patterns as indicators of impending tree death in silver fir. For Ecol Manag 199:183–190

Boncina A (1999) Stand dynamics of the virgin forest Rajhenavski Rog (Slovenia) during the past century. In: Diaci J (ed) Virgin forests and forest reserves in Central and East European countries: history, present status and future development: proceedings of the invited lecturers' reports presented at the COST E4 management committee and working groups meeting in Ljubljana, Slovenia. Biotechnical faculty, Department of Forestry and Renewable Forest Resources, Ljubljana, pp 95–110

Boncina A (2000) Comparison of structure and biodiversity in the Rajhenav virgin forest remnant and managed forest in the Dinaric region of Slovenia. Glob Ecol Biogeogr 9:201–211

Boncina A, Diaci J, Cencic L (2002) Comparison of the two main types of selection forests in Slovenia: distribution, site conditions, stand structure, regeneration and management. Forestry 75(4):365–373

Boncina A, Gaspersic F, Diaci J (2003) Long-term changes in tree species composition in the Dinaric mountain forests of Slovenia. Forestry Chron 79(2):227–232

Cavlovic J (2000) Novi program gospodarenja za G.J. Belevine (2000–2009)—zaustavljanje nepovoljnih trendova i iniciranje povoljnih procesa u razvoju preborne sume? Sumarski list 124(7–8):450–457

Cavlovic J, Bozic M, Boncina A (2006) Stand structure of an uneven-aged fir-beech forest with an irregular diameter structure: modeling the development of the Belevine forest, Croatia. Eur J For Res 125:325–333

Chapman RA, Heitzman E, Shelton MG (2006) Long-term changes in forest structure and species composition of an upland oak forest in Arkansas. For Ecol Manag 236(1):85–92

Debeljak M, Dzeroski S, Adamic M (1999) Interactions among the red deer (*Cervus elaphus* L.) population, meteorological parameters and new growth of the natural regenerated forest in Sneznik, Slovenia. Ecol Model 121:51–61

Diaci J (2006) Gojenje gozdov: pragozdovi, sestoji, zvrsti, nacrtovanje, izbrana poglavja (in Slovene). Biotechnical faculty, Department of Forestry and Renewable Forest Resources, Ljubljana

Duchesne L, Ouimet R, Moore JD, Paquin R (2005) Changes in structure and composition of maple-beech stands following sugar maple decline in Quebec, Canada. For Ecol Manag 208(1–3):223–236

Fabjan I (1956) Snezniska jelenjad. Lovec 39(6):161–169

Ficko A, Boncina A (2006) Silver fir (*Abies alba* Mill.) distribution in Slovenian forests. Zbornik gozdarstva in lesarstva 79:19–35

FMP (1912) Betriebseinrichtung für das Dezennium 1912–1921. Reviere Schneeberg, Leskova dolina, Masun, Georgstal (in German)

FMP (1936) Forest management plan for FMU Leskova dolina 1936 (in Italian)

FMP (1954) Forest management plan for FMU Leskova dolina 1954–1963 (in Slovene)

FMP (1964) Forest management plan for FMU Leskova dolina 1964–1973 (in Slovene)

FMP (1974) Forest management plan for FMU Leskova dolina 1974–1983 (in Slovene)

FMP (1994) Forest management plan for FMU Leskova dolina 1994–2003 (in Slovene)

FMP (2004) Forest management plan for FMU Leskova dolina 2004–2013 (in Slovene)

Frelich LE, Lorimer CG (1985) Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. Biol Conserv 34(2):99–120

Gaspersic F (1967) Razvojna dinamika mesanih gozdov jelke-bukve na Snezniku v zadnjih sto letih (in Slovene). Gozdarski vestnik 7–8:202–237

Gaspersic F (1974) Zakonitosti naravnega pomlajevanje jelovo-bukovih gozdov na visokem krasu Sneznisko-Javorniskega masiva: doctoral dissertation (in Slovene). Biotechnical faculty, Department of Forestry and Renewable Forest Resources, Ljubljana

Gill RMA (1992a) A review of damage by mammals in north temperate forests. 1. Deer. Forestry 65(2):145–169

Gill RMA (1992b) A review of damage by mammals in north temperate forests. 3. Impact on trees and forests. Forestry 65(4):363–388

Heuze P, Schnitzler A, Klein F (2005) Consequences of increased deer browsing winter on silver fir and spruce regeneration in the Southern Vosges Mountains: implications for forest management. Ann For Sci 62(2):175–181

Hollander M, Wolfe DA (1999) Non-parametric statistical methods, 2nd edn. Wiley, New York

Hufnagl L (1893) Der Plenterwald, sein Normalbild, Holzvorrat, Zuwachs und Ertrag. Österr Vierteljahresschr Forstwes 117–132

Jarni K, Robic D, Boncina A (2004) Analysis of the influece of ungulates on the regeneration of Dinaric fir-beech forests in the research site Trnovec in the Kocevje forest management region. Zbornik gozdarstva in lesarstva 74:141–164

Jerina K (2006) Spatial distribution, home range and body mass of red deer (*Cervus elaphus* L.) in regard to environmental factors: doctoral dissertation (in Slovene). Biotechnical faculty, Department of Forestry and Renewable Forest Resources, Ljubljana

Jerina K (2008) Velika rastlinojeda divjad in razvojna dinamika gozdnih ekosistemov: proucevanje vplivov izbranih okoljskih in populacijskih parametrov ter gozdno-gojitvenih sistemov na zmoznosti naravne obnove: zakljucno porocilo o rezultatih opravljenega raziskovalnega dela na projektu v okviru ciljnega raziskovalnega projekta (CRP) "Konkurencnost Slovenije 2006–2013": Research report. Biotechnical faculty, Department of Forestry and Renewable Forest Resources, Ljubljana

Johann E (2007) Traditional forest management under the influence of science and industry: the story of the alpine cultural landscapes. For Ecol Manag 249(1–2):54–62

Korpel S (1995) Die Urwälder der Westkarpaten. Gustav Fisher Verlag, Stuttgart

Krofel M, Kos I, Linnell J, Odden J, Teurlings I (2008) Human kleptoparasitism on Eurasian lynx (*Lynx lynx* L.) in Slovenia and Norway. Varstvo narave 21:93–103

Larsen JB (1995) Ecological stability of forests and sustainable silviculture. For Ecol Manag 73(1–3):85–96

Linder P (1998) Structural changes in two virgin boreal forest stands in central Sweden over 72 years. Scand J For Res 13(4):451–461

Linder P, Östlund L (1998) Structural changes in three mid-boreal Swedish forest landscapes, 1885–1996. Biol Conserv 85(1–2): 9–19

Montes F, Sánchez M, del Rio M, Canellas I (2005) Using historic management records to characterize the effects of management on the structural diversity of forests. For Ecol Manag 207(1–2):279–293

Moore PD, Webb JA, Collinson ME (1997) Pollen analysis. Blackwell, London

Motta R (1996) Impact of wild ungulates on forest regeneration and tree composition of mountain forests in the Western Italian Alps. For Ecol Manag 88(1–2):93–98

O'Hara KL, Hasenauer H, Kindermann G (2007) Sustainability in multi-aged stands: an analysis of long-term plenter systems. Forestry 80:163–181

Oliver CD, Larsen BC (1996) Forest stand dynamics. Wiley, New York

Ott E (1989) Verjüngungsprobleme in hochstaudenreichen Gebirgsnadelwäldern. Schweizerische Zeitung Forstwes 140(1):23–42

Perko F (2002) Zapisano v branikah: Gozdovi in gozdarstvo od Sneznika do Nanosa skozi cas. Gozdarsko drustvo Postojna, Postojna

Petit CC, Lambin EF (2002) Long-term land -cover change in the Belgian Ardennes (1775–1929): model-based reconstruction vs. historical maps. Glob Change Biol 8:616–630

Pickett ST, White PS (1985) The ecology of natural disturbance of natural patch dynamics. Academic Press, San Diego

Pintaric K (1978) Urwald Perucica als natürliches Forschungslaboratorium. Allgemeine Forst Zeitschrift 24:702–707

Prpic B, Matic S, Vukelic J, Seletkovic Z (2001) Virgin forests of beech and fir in the Croatian Dinaric Mountain range. In: Prpic B (ed) Silver fir (*Abies alba* Mill.) in Croatia. Akademija sumarskih znanosti, Hrvatske sume, p.o. Zagreb, Zagreb, Croatia, pp 479–500

Putman RJ (1996) Ungulates in temperate forest ecosystems: perspectives and recommendations for future research. For Ecol Manag 88(1–2):205–214

Rabotnov TA (1992) Phytozönologie: Struktur und Dynamik natürlicher Ökosysteme. Verlag Eugen Ulmer, Stuttgart

Radeloff VC, Mladenoff DJ, He HS, Boyce MS (1999) Forest landscape change in the northwestern Wisconsin Pine Barrens from pre-European settlement to the present. Can J For Res 29(11):1649–1659

Roseberry JL, Woolf A (1991) A comparative evaluation of techniques for analyzing white-tailed deer harvest data. Wildlife monographs 117

Schollmayer H (1906) Direktiven für die Bestandesaufnahme und die Betriebseinrichtung auf der F.C. Herrschaft Schneeberg. Kleinmayr—Bamberg, Ljubljana

Schütt P, Weisberger H, Lang UM, Roloff A, Stimm B (1999) *Abies alba* Miller, 1768. In: Schütt P, Roloff A (eds) Enzyclopädie der Holzgewächse: Handbuch und Atlas der Dendrologie, 16. Ergänzungslieferung. Wiley-VCH, Weinheim

Schütz JP (2001) Der Plenterwald und weitere Formen strukturierter und gemischter Wälder. Parey, Berlin

Schweingruber FH (1996) Tree rings and environment. Dendroecology. Swiss Federal Institute for Forest, Snow Landscape Research, Birmensdorf, Paul Haupt Verlag, Berne

Senn J, Suter W (2003) Ungulate browsing on silver fir (*Abies alba*) in the Swiss Alps: beliefs in search of supporting data. For Ecol Manag 181(1–2):151–164

Sercelj A (1996) The origins and development of forests in Slovenia. Slovenska akademija znanosti in umetnosti, Ljubljana

Simak M (1951) Untersuchungen über den naturlichen Bauartenwechsel in der schweizerischen Plenterwälder. Mitteilungen Eidgenosischen Anstalt für Forstlichen Versuchswessen 27:406–468

Smith DW, Drummer TD, Murphy KM, Guernsey DS, Evans SB (2004) Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. J Wild Manag 68:153–166

Swetnam TW, Allen CD, Betancourt JL (1999) Applied historical ecology: using the past to manage for the future. Ecol Appl 9:1189–1206

van der Maarel E (2005) Vegetation ecology. Blackwell, Malden

Veselic Z (1991) Na Postojnskem prestevilna divjad se naprej hudo ogroza gozdno mladje. Gozdarski vestnik 49:147–157

Vrska T, Adam D, Hort L, Kolár T, Janík D (2009) European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) rotation in the Carpathians—a developmental cycle or a linear trend induced by man? For Ecol Manag 258(4):347–356

Webb NF, Hebblewhite M, Merrill EH (2008) Statistical methods for identifying wolf kill sites using global positioning system locations. J Wild Manag 72:798–807

2.3 NATURAL DISTURBANCES IN NORWAY SPRUCE DOMINATED FORESTS IN THE JULIAN ALPS: THEIR EXTENT, INFLUENTIAL FACTORS AND IMPORTANCE IN FOREST STAND DYNAMICS

Klopčič M., Poljanec A., Bončina A. Natural disturbances in Norway spruce dominated forests in the Julian Alps: their extent, influential factors and importance in forest stand dynamics. = [Naravne motnje v zasmrečenih gozdovih v Julijskih Alpah: njihov obseg, vplivni dejavniki in pomen za razvoj gozdov]. Unpublished paper = (neobjavljeno)

Natural disturbances in Norway spruce dominated forests in the Julian Alps: their extent, influential factors, and importance in forest stand dynamics

KLOPČIČ, Matija [1], POLJANEC, Aleš [2], BONČINA, Andrej [3]

[1] K.M., corresponding author, University of Ljubljana, Biotechnical Faculty, Department of Forestry and Renewable Forest Resources, Vecna pot 83, 1000 Ljubljana, Slovenia, e-mail address: matija.klopcic@bf.uni-lj.si, phone: 0038613203551, fax: 0038612571169

[2] dr. P.A., University of Ljubljana, Biotechnical Faculty, Department of Forestry and Renewable Forest Resources, Vecna pot 83, 1000 Ljubljana, Slovenia, e-mail address: ales.poljanec@bf.uni-lj.si, phone: 0038613203508

[3] prof. dr. B.A., University of Ljubljana, Biotechnical Faculty, Department of Forestry and Renewable Forest Resources, Vecna pot 83, 1000 Ljubljana, Slovenia, e-mail address: andrej.boncina@bf.uni-lj.si, phone: 0038613203500

ABSTRACT

The extent of windthrows, snow breakages, insect outbreaks, and other natural disturbances, their influential factors, and their importance in long-term forest stand dynamics were studied in Norway spruce-dominated forest in the Bled forest region and in the Jelovica study area. A GIS database was created on a compartment spatial level and included sanitary cutting due to different reasons as the dependent variables and forest stand characteristics, site conditions, and past forest management measures as potential predictors. The occurrence of a natural disturbance was adopted if more than 1% of stand volume was damaged. The extent of natural disturbances and their importance in the stand dynamics were examined using basic statistical analysis of their frequency and severity. Relations between the natural disturbance occurrences and single indpendent variables were investigated with univariate binary logistic regression for continuous independent variables and contingency tables and chi-square tests for categorical variables. In the Bled forest region, moderate-severity disturbances had a substantial increasing influence on the total annual cut in 1904-2006. In the Jelovica study area, 318 windthrows, 279 snow breakages, 324 insect outbreaks, and 109 salvage cut due to other reasons were registered in 1979-2010. Most registered disturbances were of low severity, although some windthrows were also classified as moderate and high-severity. In 1979-2010 the annual salvage cut averaged 50.3 % of the total annual cut. Among stand characteristics, dbh structure, developmental phases or forest types, and tree species composition were found to be important influential factors in various natural disturbance occurrences. Among site conditions, aspect, variation of the aspect within a compartment, and rockiness were significantly related to all three analysed natural disturbances, which was also the case for both past forest management events. Disturbance regimes, the role of natural disturbances in spruce-dominated mountainous forests, and factors related to natural disturbance occurrence are discussed, and some implications for forest management are proposed.

INTRODUCTION

Forest stand dynamics result from a complex interplay of site conditions, inter- and intraspecific relationships, and natural and human-induced disturbances (Oliver and Larsen, 1996). Natural disturbances are defined as relatively discrete events that disrupt the ecosystem, community, or population and change the resources, substrate availability, or physical environment (Pickett and White, 1985). They represent an important factor driving forest stand dynamics (Frelich, 2002); however, their importance (i.e. frequency and severity) may vary over time and space. In the last century, an increase in the frequency and severity of natural disturbances has already been observed (e.g. Schelhaas et al., 2003), and this trend is expected to intensify in the coming decades as a consequence of global climate change (Dale et al., 2001; Fuhrer et al., 2006; Schumacher and Bugmann, 2006).

The importance of natural disturbances in forest stand dynamics as well as the main disturbance agents differ between forest types (Pickett and White, 1985; Anko, 1993; Frelich, 2002). The role of natural disturbances in different forest types and the influence of site and forest stand factors on natural disturbance regimes have been well investigated (e.g. Pickett and White, 1985; Attiwill, 1994; Nykänen et al., 1997; Ulanova, 2000; Wermelinger et al., 2002; Wermelinger, 2004; Nagel et al., 2007), but there are few studies concerning natural disturbance regimes based on long-term historical data sets (e.g. Schieser, 1997; Dorland et al., 1999; Schelhaas et al., 2003; Nilsson et al., 2004). However, some studies investigated natural disturbance regimes and their characteristics in altered Norway spruce-dominated forests (e.g. Hanewinkel et al., 2008; Klopčič et al., 2009). Among natural disturbance agents, wind (Stathers et al., 1994; Ruel, 2000; Dvorak et al., 2001; Kramer et al., 2001; Dobbertin, 2002; Ogris et al., 2004; Bachmann and Dvorak, 2005; Mayer et al., 2005; Splechtna et al., 2005; Schütz et al., 2006; Evans et al., 2007; Nagel et al., 2007) and fire (e.g. Pickett and White, 1985; Attiwill, 1994; Oliver and Larsen, 1996; Schumacher and Bugmann, 2006; Genries et al., 2009) have been the most exhaustively studied, followed by insect outbreaks (e.g. Wermelinger et al., 2002; Wermelinger, 2004; Gilbert et al., 2005; Seidl et al., 2007). Less attention has been given to snow breakage (e.g. Nykänen et al., 1997; Jalkanen and Mattila, 2000; Pellikka and Järvenpää, 2003), other reasons such as ice storms, pollution, avalanches, fungi, etc. (e.g. Picket and White, 1985; Attiwill, 1994), and interactions among different disturbance agents (e.g. Veblen et al., 1994; Hanewinkel et al., 2008; Klopčič et al., 2009). In mountain forests of the European temperate zone, wind, snow, and insects (mainly bark beetles) seem to be the main natural disturbance agents (Schelhaas et al., 2003; Hanewinkel et al., 2008), but fire (Schumacher and Bugmann, 2006; Wick and Möhl, 2006; Genries et al., 2009) and large ungulates (Gill, 1992) might also have a noticeable effect in the long-term.

A large proportion of mountain forests in Central Europe were changed in the past due to intensive anthropogenic disturbances, i.e. forest management (Johann, 2007). In many regions the tree species composition and stand structure of mountain forests were substantially modified towards even-aged Norway spruce (*Picea abies* (L.) Karst.) dominated forest stands (Ott et al., 1997; Spiecker et al., 2004). The altered structure and composition of forest stands led to lower resistance of these forests and consequently to greater damage caused by natural disturbances (Schelhaas et al., 2003; Spiecker et al., 2004). However, even regionally, changes in the structure and composition of forest stands differed in their intensity and extent (Klopčič and Bončina, 2011), and, in this respect, the resistance of forest stands may also vary on a regional or even forest stand spatial scale.

The recognition of altered patterns of forest stand dynamics in mountain forests and differences between them on a regional spatial scale are of great importance when close-to-nature, sustainable, and multifunctional forest management (e.g. Bončina, 2009) is applied. The main goal of such an approach to forest management is to create forest stands that sustainably provide desired economic, ecological, and social functions while taking into consideration the site conditions and natural processes in these stands. Moreover, one of the aims of ecosystem-oriented forest management is to minimize the forest management hazards (Diaci and McConnell, 1996) due to natural disturbances. To reach this goal, we need to recognize the patterns of forest stand dynamics. Furthermore, their recognition represents the basis for the selection of silvicultural measures, which might increase the resistance and resilience of forest stands to future natural disturbances.

Alpine silver fir (*Abies alba* Mill.)-European beech (*Fagus sylvatica* L.) forests (*Homogyne sylvestris-Fagetum* Marinček et al. 1993) of pronounced economic and ecological functions, as well as social forest functions, are widely spread in the Slovenian Alps. Despite a 50-year long tradition of close-to-nature forest management in the region, the natural tree species composition of forests has changed noticeably due to past forest management that practiced clear-cutting and planting of Norway spruce (Veber, 1986). The result of the latter are current Norway spruce-dominated forest stands in which forest damage caused by natural disturbances represents an obvious impediment to planned forest management (FMP Bled, 2003). In the past a relatively large amount of attention has been devoted to natural disturbance research in the alpine region (e.g. Wraber, 1950; Bernik, 1966; Deanković, 1969; Zupančič, 1969; Bleiweis, 1983). But recently it has gained much less attention (Ogris et al., 2004; Firm et al., 2009; Klopčič et al., 2009; Jakša and

Kolšek, 2010) despite a general knowledge of their high importance in managed (e.g. Schelhaas et al., 2003; Hanewinkel et al., 2008) and unmanaged mountain forests (e.g. Splechtna et al., 2005; Nagel et al., 2007).

The aims of our study were thus 1) to examine the regime of the main natural disturbances (i.e. windthrow, snow breakage, and insect outbreaks) in spruce dominated forest stands in the last century, 2) to determine the influence of selected site and stand variables and past forest management on the occurrence of natural disturbance, and 3) to discuss the role of natural disturbance in the long-term stand dynamics of the analysed forests.

METHODS

STUDY AREA

Two study areas in the Julian Alps were considered in the analysis: 1) the Bled forest region and 2) forest management unit (FMU) Jelovica (Figure 1). The Bled forest region comprised approximately 6,400 ha of mountain forests in two FMUs, Mežaklja and Pokljuka. Forests of the Bled forest region have been mainly state or church owned. They were intensively managed throughout the entire observed period. Secondary Norway spruce dominated forests prevail, but natural, pure Norway spruce forests and mixed silver fir-European beech-Norway spruce forests are also present. The main forest characteristics are a high proportion of mature stands and a high average stand volume.

Our main study area was the Jelovica FMU, which encompasses 4792 ha of mainly mixed silver fir-European beech-Norway spruce forests characterised by dominance of the latter and a high average stand volume (Table 1). Forests in the FMU are divided into 231 (sub)compartments which underwent negligible changes in the period 1979-2010. Elevation ranges from 480 to 1667 m a.s.l. and averages approximately 1200 m a.s.l. The prevalent parent materials are limestone and dolomite on which mainly eutric cambisols and rendzinas evolved. The mean annual temperature averages 5.5 °C and average annual precipitation amounts to 2338 mm. The prevailing winds blow from the southwest, west, and northwest.

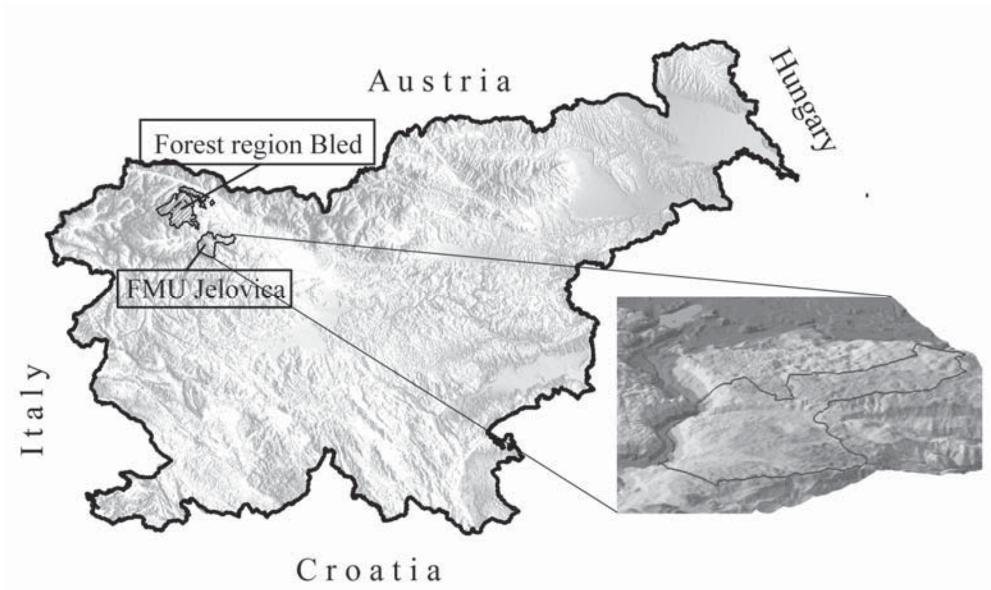

Figure 1: The locations of the study areas, the Bled forest region and the Jelovica forest management unit, including topography

Table 1: Characteristics of the Jelovica FMU in the period 1983-2002

		Year of forest inventory		
	Unit	1983	1992	2002
Forest area	ha	4813	4710	4814
Mean (sub)compartment area	ha	20.5	20.0	20.6
Average stand volume	$m^3 ha^{-1}$	305	318	346
Proportion in stand volume				
diameter class 10-29 cm	%	36	39	38
diameter class 30-49 cm	%	45	42	40
diameter class ≥50 cm	%	19	19	22
Average volume increment	$m^3 ha^{-1} y^{-1}$	-	7.3	8.4
Proportion in stand volume				
Norway spruce	%	70	75	73
silver fir	%	13	9	9
European beech	%	17	14	16
sycamore	%	0	2	2

DATABASE CREATION

For the Bled forest region, data on total annual cut and annual salvage cuts due to windthrow and snow breakage were gathered from archival forest management plans (FMP) and annual harvesting books for the period 1904-2006, preserved in the archives of the Slovenia Forest Service. Similarly, the data on salvage cuts due to several reasons in the Jelovica FMU were gathered for the period 1979-2010, and a GIS database was created at a compartment spatial level. It included several dependent and 21 independent variables of forest stand characteristics, site conditions, and past forest management events (Table 2). Each row in the database representing dependent and independent variables in a compartment in a single year was called an event in our study.

Table 2: Independent site, stand, and past forest management variables included in the analysis

Group of factors	Variable	Varible type[a]	Units	Description of the variable
Site characteristics	INC	con.	°	Mean inclination
	INC_STD	con.	/	Standard deviation of inclination within a compartment
	ELV	con.	m a.s.l.	Mean elevation
	ELV_STD	con.	/	Standard deviation of elevation within a compartment
	ASP	cat.	1–9	Aspect (1-N;2-NE;...;9-plane)
	ASP_VAR	con.	/	Variation of aspect within a compartment
	TOP	cat.	1–4	Topographic position (1-plane;2-foot of the hills;3-slope;4-ridge)
	STO	con.	%	Bedrock (stone) cover
	ROC	con.	%	Rock cover
Stand characteristics	VOL_A	con.	m^3 ha^{-1}	Volume of small diameter trees (dbh < 30 cm)
	VOL_B	con.	m^3 ha^{-1}	Volume of medium diameter trees (30 ≤ dbh < 50 cm)
	VOL_C	con.	m^3 ha^{-1}	Volume of large diameter trees (dbh ≥ 50 cm)
	Y_GR	con.	%	Proportion of young growth in a compartment
	PO_ST	con.	%	Proportion of pole stands in a compartment
	MT_ST	con.	%	Proportion of mature stands in a compartment
	RG_ST	con.	%	Proportion of regeneration stands in a compartment
	UE_ST	con.	%	Proportion of uneven-aged stands in a compartment
	P_SP	con.	%	Proportion of Norway spruce in a compartment
	P_BR	con.	%	Proportion of broadleaves in a compartment
Past events	PR_DS	cat.	0–1	Natural disturbance occurrence within previous 5 years
	PR_CT	cat.	0–1	Presence of regular cutting within previous 5 years

[a] : con. – continuous variable; cat. – categorical variable

The basic dependent variables were annual salvage cuts due to windthrow, snow breakage, insect outbreaks, and other reasons. Based on them, the disturbance index DI_X with X representing a particular disturbance agent (W windthrow, S snow breakage, I insect outbreak, O other reasons) was calculated for each compartment in each year as the proportion of stand volume damaged by a particular natural disturbance agent. The disturbance indices were then recoded into categorical variables D_X with seven categories: 1, <0.01; 2, 0.01-0.029; 3, 0.03-0.099; 4, 0.10-0.199; 5, 0.20-0.399; 6, 0.40-0.699; 7, 0.70-1.00. In our study a disturbance index of 1 % (DI_X=0.01) was adopted as the threshold that determined the occurrence of a natural disturbance. Considering this, a new dependent binary variable for each disturbance agent DO_X was established with a value of 0 representing category 1 of D_X and the value of 1 representing categories 2-7 of D_X. The threshold value of 1 % damaged stand volume allowed us to exclude very small-scale disturbances (a damage of one or few trees) from the analysis.

Forest stand characteristics were derived mainly from forest inventory data in the FMPs. Within each compartment the value of stand volume was updated for each year in a 10-year inventory period considering the stand volumes at the beginning and the end of the inventory period, the amount of annual volume increment, and total annual cut. Horizontal structure of forests was denoted by the proportions of developmental phases in a compartment, which were derived from archival and current forest stand maps.

Site conditions were derived mainly from a digital elevation model with a spatial resolution of 25 m and an average height accuracy of 1.5-6.5 m; only stoniness and rockiness were adopted from forest inventory data in the FMPs.

Past forest management events were characterized by two dichotomous variables: previous natural disturbance (PR_DS) and previous regular cuts (PR_CT). The PR_DS was defined as the occurrence of disturbance(s) of any type in any of the previous 5 years with severity ≥1 % of the stand volume. Similarly, the PR_CT was defined as the occurrence of regular cut in any of the previous 5 years.

DATA ANALYSIS

Natural disturbances were examined in their frequency and severity. Windthrows and snow breakages were investigated at both spatial levels in the Bled forest region and in the Jelovica FMU, while insect outbreaks and disturbances due to other reasons were studied only in the Jelovica FMU. The frequency was expressed as the relative frequency of all events. It was examined graphically and in regard to the severity of natural disturbances. The severity of natural disturbances was defined as 1) the proportion of damaged stand volume in a single year, and 2) the proportion of salvage cut due to a particular reason in the total annual cut. The terms describing the severity of natural disturbances were adopted after Frelich (2002: p. 16), but were modified to meet the needs of our research. An event with DI_X of 1–9.9 % was determined as a low-severity disturbance, an event with DI_X of 10–69.9 % as a moderate- severity disturbance, and an event with DI_X of 70–100 % as a high-severity disturbance.

Relations between the occurrence of the main natural disturbances (windthrows, snow breakages, and insect outbreaks) and single independent variables were investigated with univariate logistic regression (Hosmer and Lemeshow, 2000) if the independent variable was a continuous one, while chi-square analysis of r×k contingency table (Zar, 2010) were applied if the independent variable was a categorical (or binary) one. In both methods the relations between dependent and independent variables were found to be significant if the p-value was lower than α=0.05 (95 % confidence level). For continuous independent variables the probability P of natural disturbance occurrence was then calculated based on the logistic regression model according to the following equation 1:

$$P = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n)}{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n)} \quad \ldots (1)$$

RESULTS

THE EXTENT OF NATURAL DISTURBANCES

In the Bled forest region, natural disturbances had diverse influences on the total annual cut in 1904-2006 (Figure 2). Moderate-severity disturbances, such as those in 1922, 1961, or 2006, had a substantial increasing influence on the total annual cut, while the influence of low-severity disturbances on the amount of annually cut timber was not so obvious. The frequency of natural disturbances, especially windthrows, has increased in the last three decades.

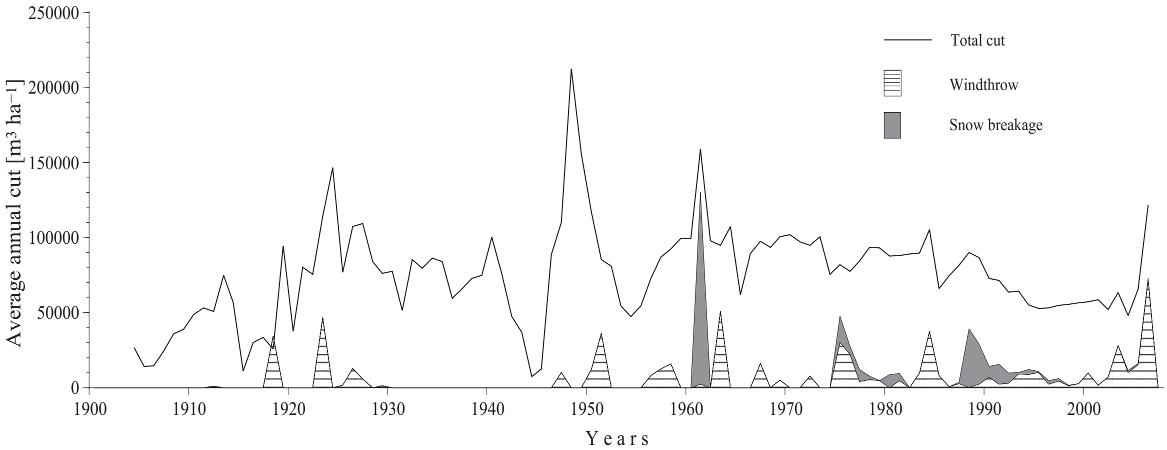

Figure 2: Annual total cut with salvage cut due to windthrow and snow breakage in state owned spruce-dominated forests in the Bled forest region, 1904-2006

In the period 1979-2010, 318 windthrows, 279 snow breakages, 324 insect outbreaks, and 109 salvage cuts due to other reasons were registered in the Jelovica FMU. Among all events, mainly events treated as non-occurrence of natural disturbance (damaging less than 1 % of total stand volume) were recorded (Figure 3). Most of the registered disturbances were of low severity, i.e. 276 windthrows (87 % of all windthrows), 272 (97 %) snow breakages, 322 (99 %) insect outbreaks, and 106 (99 %) salvage cuts due to other reasons. In the same period, eighteen windthrows out of 318 occurred, blowing down 20 % or more of the total stand volume, while no snow breakages or insect outbreaks were recorded with such severity. In six events a high-severity windthrow occurred (≥70 % of total stand volume were damaged).

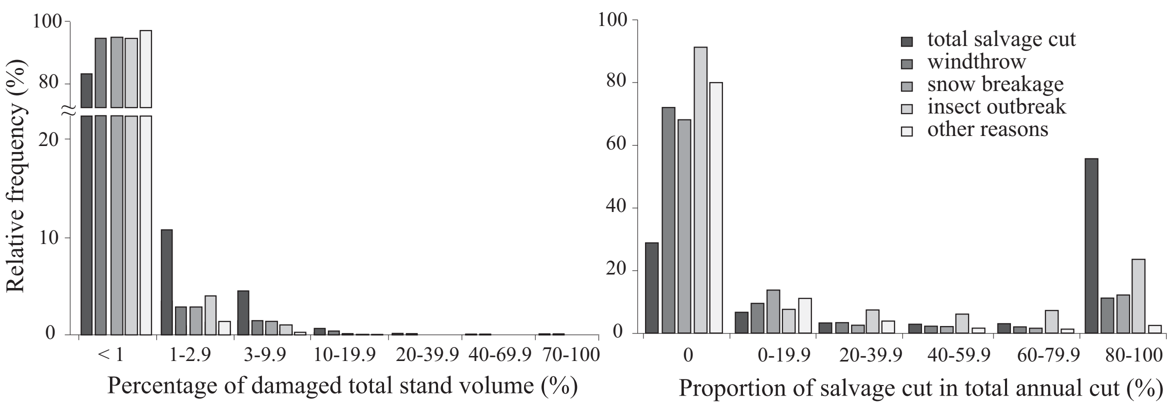

Figure 3: The relative frequency of events in regard to their severity expressed as damages of total stand volume (A) and proportion in total annual cut (B)

In 1979-2010 the average annual salvage cut amounted to 2.90 m^3 ha^{-1} representing 50.3 % of the average total annual cut (5.77 m^3 ha^{-1}), with windthrows, snow breakages, insect outbreaks, and salvage cut due to other reasons amounting to 1.04, 0.78, 0.83, and 0.25 m^3 ha^{-1} y^{-1}, respectively. When the proportion of total salvage cut in the total annual cut was considered, the highest proportion of events (56 % out of 3311 events with registered cut) were observed in the 80-100 % class (Figure 3), but were much lower for single disturbances. This result indicated that sequential or concurrent natural disturbances caused by different agents often occurred in the same compartment, reflected in their aggregated damaging effects. In contrast, in single disturbances the most represented class was that of 0 % proportion of salvage cut in the total annual cut. However, single disturbances sometimes represented more than 80 % of the total annual cut in a compartment. This happened in 369 (11 % of all events with registered cut) events with registered windthrow, 402 (12 %) events with registered snow breakage, 545 (16 %) events with recorded insect outbreaks, and 80 (2 %) events with salvage cut due to other reasons.

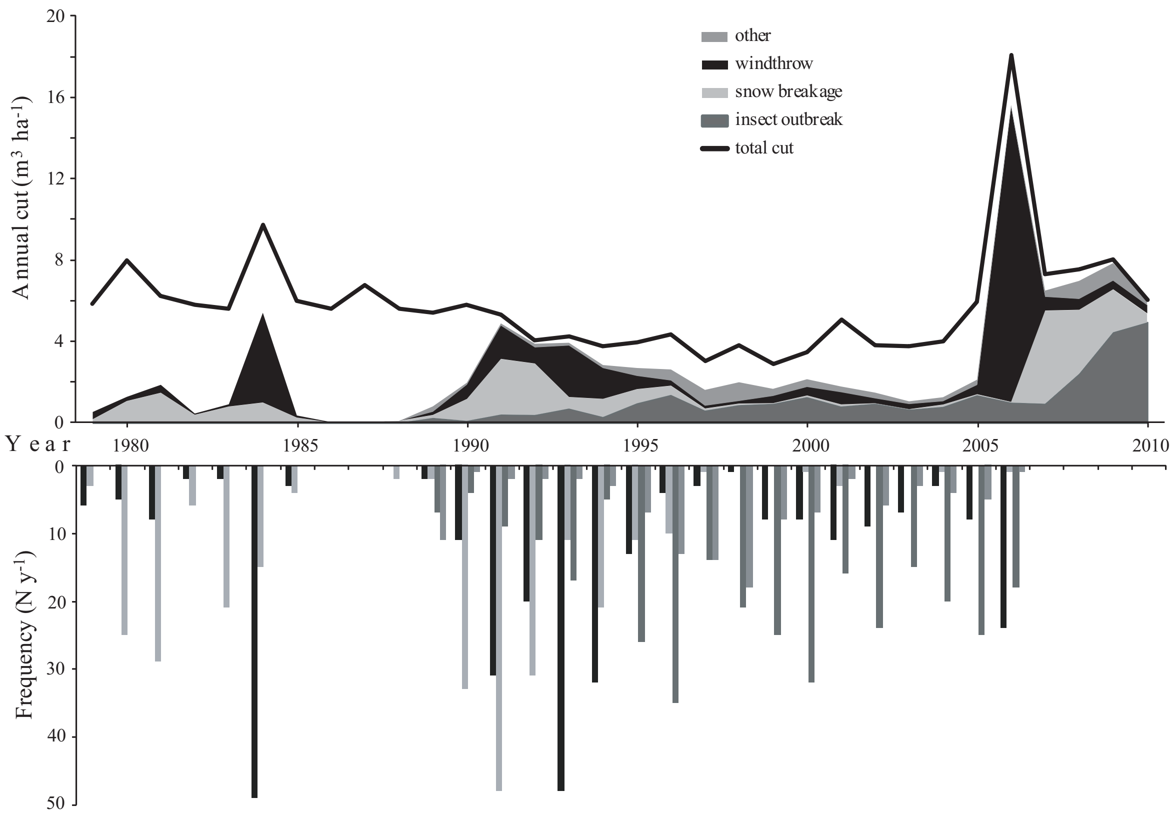

Figure 4: The importance of natural disturbances in forest management in the Jelovica FMU, 1979-2010: the amount of annual salvage cut and the frequencies of natural disturbances (for 2007-2010 only data on total annual cut due to different reasons were gathered)

The frequency and severity of natural disturbances (at least insect outbreaks), seems to have increased in the last decade (Figures 2 and 4). The importance of windthrow disturbance was noticeable through the entire observation period. A high frequency of windthrow events was observed in 1984, 1991, 1993, and 1994, causing in total only moderate-severity disturbances. In contrast, the highest-severity windthrow happened in 2006, but the frequency of disturbance events was not so high since the windthrow was concentrated and a lower number of compartments were heavily damaged. Snow breakage was also registered throughout the entire observation period with peaks in frequency and severity in 1981, 1990-1992, and 2007-2009. The severity and extent of insect outbreaks were greater after 1990, especially moderate- and high-severity outbreaks after 2007. Also, the frequency and amount of salvage cut timber due to other reasons increased after 1990.

FACTORS RELATED TO NATURAL DISTURBANCE OCCURRENCES

Many site, stand, and past forest management variables were significantly associated with natural disturbance occurrences (Table 2).

Almost all analysed stand variables were significantly related to all three main natural disturbances, but their influences on the occurrence of natural disturbance were diverse. The probability of windthrow occurrence was most significantly increased by increasing values of large-diameter (dbh≥50 cm) trees, the proportion of young growth, the proportion of stands in regeneration, and the proportion of spruce in the total stand volume (Figure 5), while it was decreased by the proportion of pole-stage and uneven-aged stands. Very similar results were obtained for insect outbreak occurrence. On the contrary, snow breakage occurrence probabilities were most significantly increased by the proportion of pole-stage and mature stands and by the proportion of Norway spruce in the stand volume (Figure 5). In contrast, it was obviously decreased by increasing values of the proportion of uneven-aged stands and the proportion of broadleaves (Figure 6a).

Table 2: Factors related to natural disturbance occurence in the alpine fir-beech forests

		Windthrow	Snow breakage	Insect outbreak
Site characteristics	INC	–	√	–
	INC_STD	–	√	√
	ELV	–	√	–
	ELV_STD	–	√	√
	ASP	√	√	√
	ASP_VAR	√	√	√
	TOP	–	√	–
	STO	–	√	√
	ROC	√	√	√
Stand characteristics	VOL_A	√	√	√
	VOL_B	√	–	–
	VOL_C	√	√	√
	Y_GR	√	√	√
	PO_ST	√	√	√
	MT_ST	√	√	√
	RG_ST	√	√	√
	UE_ST	√	√	√
	P_SP	√	√	√
	P_BR	–	√	–
Past events	PR_DS	√	√	√
	PR_CT	√	√	√

* √ - relation significant at p<0.05; – - relation not significant

Several site variables were significantly related to natural disturbance occurrence, but only three variables significantly influenced all of them (Table 2; Figure 6b-d). The prevailing aspect of a compartment had a diverse influence on natural disturbance occurrence. Windthrows occurred mainly on northern to southern aspects, which are the leeward aspects, but also on sites with a western aspect, which is the most windward aspect. Greater variation of the aspect increased the probability of windthrow occurrence, while greater rockiness decreased it. Similar results were found for insect outbreaks. In contrast, snow breakages happened most frequently in sites on planes and with northeastern and eastern aspects, but also on northern and western ones. Similar to windthrows and insect outbreaks, the probability of snow breakage occurrence decreased with increasing rockiness, while increasing aspect variation within a compartment increased the probability. Elevation was only significantly related to snow breakage occurrence; the relative frequency of snow breakages dropped significantly if the elevation was above 1400 m a.s.l. (from

5.5 for elevation belt below 1200 m to 3.6 in 1200-1400 elevation belt to 0.3 for belt above 1400 m). A similar result was found for inclination; the highest frequency of snow breakages was found at the lowest inclinations (0-14.9°).

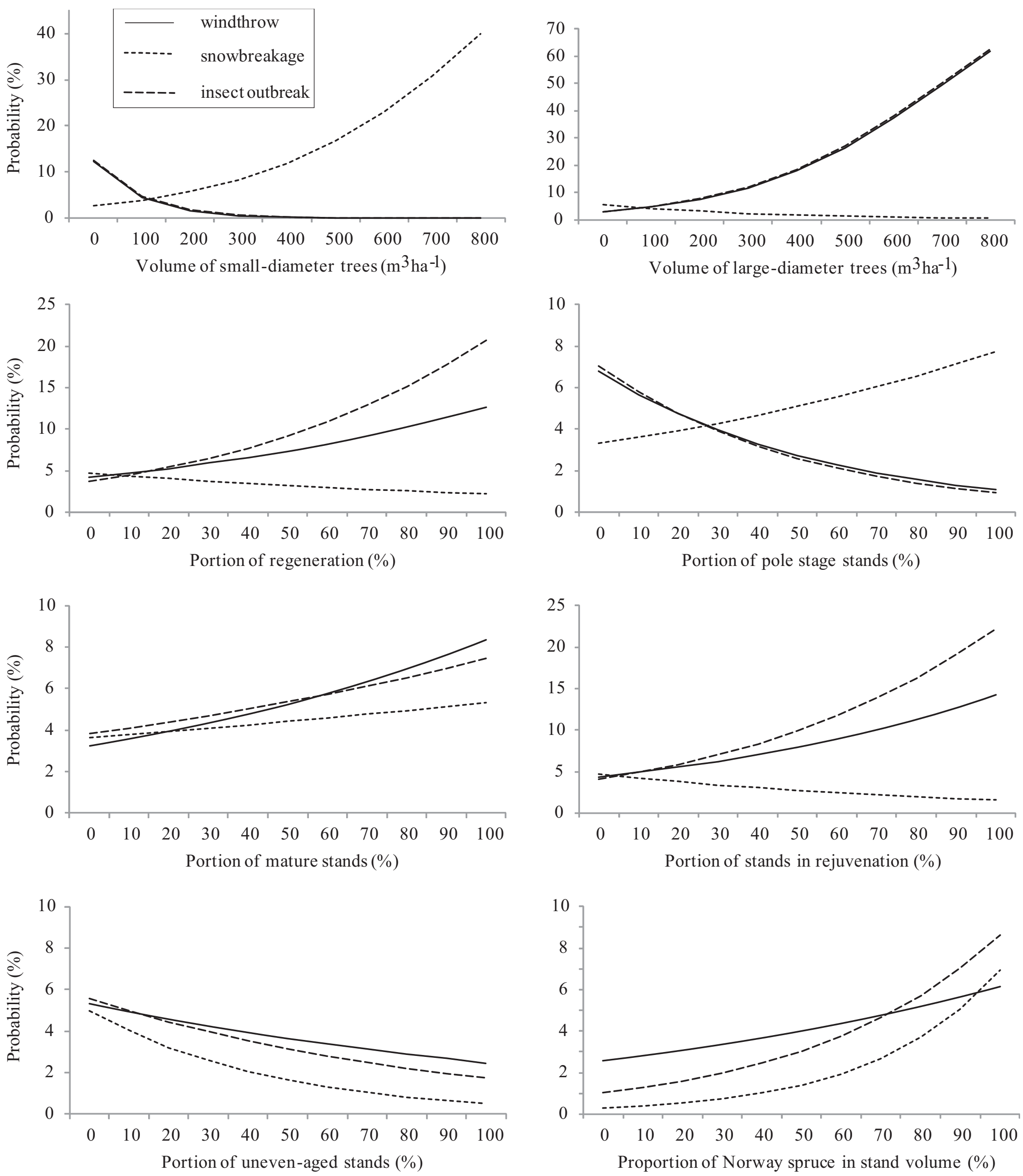

Figure 5: Probabilities of natural disturbance occurrence in relation to particular stand characteristics (only variables with significant influence on all three dependent variables are shown)

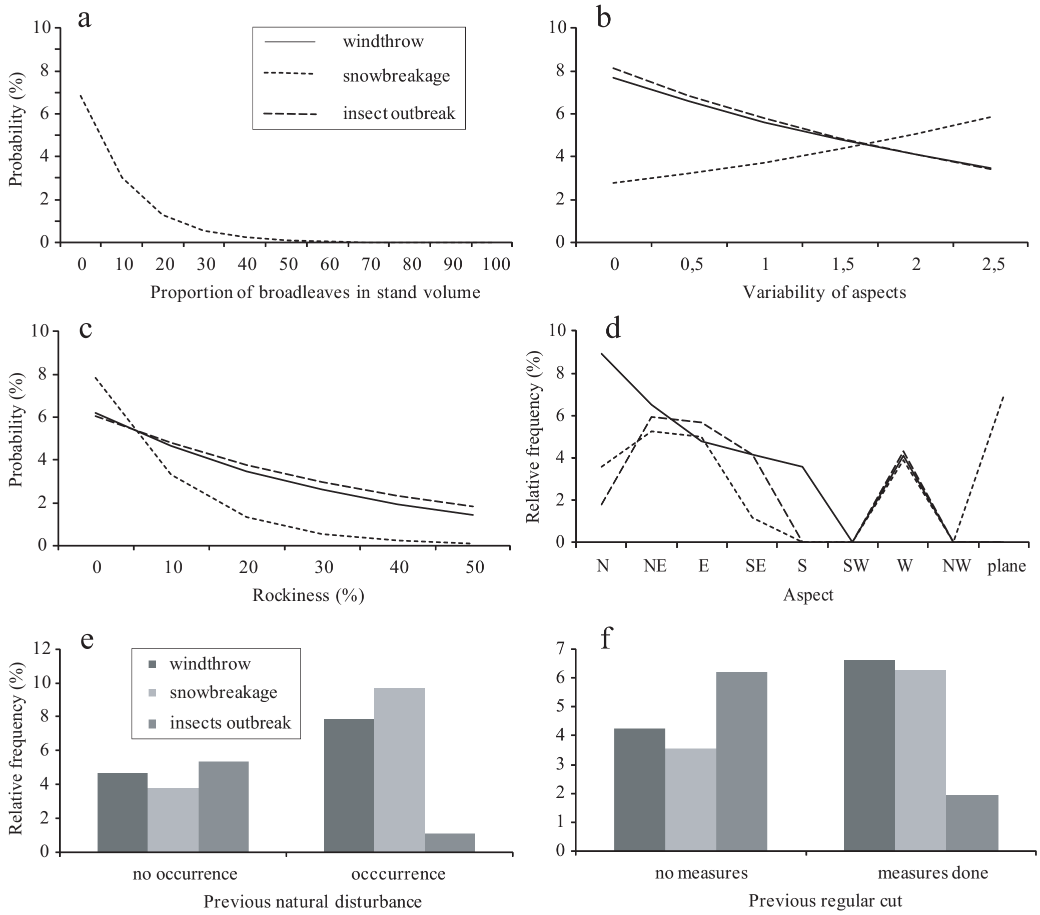

Figure 6: Probabilities of natural disturbance occurence in relation to the stand (a) and site variables (b, c), and relative frequencies of natural distrubances in relation to categorical site and past forest management variables (d-f)

Past forest management events, past regular cutting, and previous natural disturbance were significantly related to all analysed natural disturbances (Table 2; Figure 6e-f). Windthrows and snow breakages were 1.7 and 2.5 times more frequent if any natural disturbances in a compartment occurred at least once in the previous five years. Unexpectedly, under the same condition insect outbreaks occurred 4.9 times less frequently if natural disturbance did not occur before. Similar results were obtained for previous regular cuttings. Windthrows and snow breakages occurred 1.6 and 1.8 times more frequently, but insect outbreaks 3.2 times less frequently if regular cuttings were executed in the previous five years.

DISCUSSION

THE ROLE OF NATURAL DISTURBANCES IN MOUNTAINOUS SPRUCE-DOMINATED FORESTS

In Europe the total annual amount of salvage cut due to natural disturbances amounted to 35 mio m^3 of timber in the period 1950-2000 (Schelhaas et al., 2003), while in Slovenia it averaged 2.8 mio m^3 of timber in 1995-2007 (Jakša and Kolšek, 2009). In the Jelovica FMU the average annual salvage cut amounted to 2.9 m^3 ha^{-1} y^{-1} in the period 1979-2010, representing more than half of the total annual cut. A similar amount of annual total salvage cut was reported in the Black Forest in Germany (3.0 m^3 ha^{-1} y^{-1}) (Hanewinkel et al., 2008).

In our study area, like the Black Forest (Hanewinkel et al., 2008), the most important disturbance agent was wind, followed by insects and snow. Similar results have been recorded for all of Europe, but forest fires were an additional agent, causing the second highest amount of damage (Schelhaas et al., 2003): in 1950-2000 the average annual storm damage was 18.7 mio m^3 of timber (53 % in total annual salvage cut timber), followed by fire (5.5 mio m^3 or 16 %), insect outbreaks (2.9 mio m^3 or 8 %), and snow damage (1 mio m^3 or 3 %). For the latter, Nykänen et al. (1997) reported a substantially higher value of 4 mio m^3 of timber for the European Community area.

In Europe, an increasing trend in the amount of salvage cut due to natural disturbances has been especially noticeable (Mosandl and Felbermeier, 1999; Schelhaas et al., 2003; Jakša and Kolšek, 2009). The amount of damaged timber due to natural disturbances seems to have also increased significantly in the last two decades in our study area. In Europe salvage cut due to natural disturbances represented 8.1 % of the total annual cut in 1950-2000 (Schelhaas et al., 2003), while the proportion was 32 % for Slovenia in 1995-2007 (Jakša and Kolšek, 2009). In the Jelovica FMU the share of salvage cut in the total annual cut averaged 50.3 % in 1979-2010. Moreover, in the last five years the salvage cut represented the majority of the total annual cut (89–100 %). Since forest management (i.e. final and regeneration cuts, thinning, and tending) is considered to be the most important factor driving forest stand dynamics in managed forests (Oliver and Larsen, 1996; Klopčič and Bončina, 2011), the observed high proportion of salvage cut in the total annual cut indicates the important role of natural disturbances in driving forest stand dynamics of alpine silver fir-European beech forests with altered tree species composition. Moreover, in recent years forest stand dynamics has been almost exclusively driven by natural disturbances, representing a serious impediment to forest management in the study area. Consequently, forest managers have only limited options for directing forest stand dynamics towards long-term forest management goals and for ensuring the main objectives of sustainable close-to-nature forest management (Diaci and McConnell, 1996). We assume that a similar conclusion could be made for the broader alpine region, especially where natural tree species composition of forest stands has been substantially altered.

Since an increasing amount of salvage cut was observed, an increase in the frequency of natural disturbance events might be expected. But such a conclusion cannot be stated. Fluctuations in the frequency of natural disturbances have been noticed between decades or periods of a few years, as already stated earlier for windthrows (e.g. Dorland et al., 1999) and snow damage (e.g. Nykänen et al., 1997), but the increase in the frequency could not be uniformly concluded. In some regions, natural disturbances were found to be even more frequent and severe a few decades (centuries) ago than in the recent decades (e.g. Schiesser et al., 1997; Nilsson et al., 2004). Kilpeläinen et al. (2010) even stated a decrease in snow-induced damage in boreal forests after 2020. In contrast, some authors maintain that global climate change will cause more intensive occurrences of natural disturbances in the next decades (e.g. Dale et al., 2001; Fuhrer et al., 2006; Schumacher and Bugmann, 2006).

Besides climate change, another possible reason for the increasing trend in the amount of salvage cut due to natural disturbances can be found in the organisation of the forest service. A process for registering every cut tree and damaged or killed trees due to natural disturbances was already established in 1979 at the Bled Regional Unit of the Slovenian Forest Service, but has been digitised and significantly improved since then. Therefore, more reliable and accurate results could be obtained for recent years compared with the early 1980s. The other reasons can be found in the state of forest stands and changes in forest management, such as a high proportion of Norway spruce and a high stand volume associated with older forest stands (Spiecker et al., 2004; Schelhaas et al., 2003).

FACTORS RELATED TO NATURAL DISTURBANCE OCCURRENCE

Several stand, site, and past forest management variables were related to natural disturbance occurrence. However, the threshold value which determines the occurrence of a natural disturbance is always somewhat arbitrary (Hanewinkel et al., 2004). We adopted a threshold of damage of 1 % of the average stand volume in a compartment. If this value were different, the results might differ from those presented.

A high volume of large-diameter trees (dbh≥50 cm) in a stand significantly increased the probability of windthrow and insect outbreak, but not snow breakage occurrence. Similar results of increasing probabilities with increasing values of the independent variable were obtained for the proportion of mature stands, which is in close relation with the volume of large-diameter trees. Higher proportions of large-diameter trees together with increased stand volume were often found to be one of the most important factors for the increased amount of salvage cut (Mosandl and Felbermeier, 1999; Schelhaas et al., 2003; Bachmann and Dvorak, 2005; Hanewinkel et al., 2008). In contrast, the increasing volume of small-diameter trees (dbh=10-29 cm) significantly increased the probability of snow breakage, but only slightly decreased the probabilities of windthrow and insect outbreak occurrences. A similar situation was found with the proportion of pole stage stands in a compartment, which mainly comprise small-diameter trees. In confirmation, in 2007 and 2008, snow damaged 125,000 and 49,000 m^3, respectively, of mainly pole-stage (10-29 cm in dbh) spruce timber in secondary spruce forest stands, mainly in the Pokljuka and Mežaklja FMUs, but also in the Jelovica FMU (Papler-Lampe, 2008; Papler-Lampe and Kolšek, 2009). Leaning or crooked trees with only slightly tapering stems (a high height/diameter ratio) and short crowns are most prone to snow breakage, while straight, highly tapering trees with tall, live crowns are the least susceptible. The probability of snow breakage decreases in older trees (Nykänen et al., 1997; Pellikka and Järvenpää, 2003). In addition, Klopčič et al. (2009) found that wind and insects on average damage thicker trees (for both, the median was 32.5 cm in dbh), while snow breaks or uproots thinner trees (the median was 17.5 cm in dbh). A similar observation was stated by Jakša and Kolšek (2010).

Further, the analysis showed that a high portion of Norway spruce in tree species composition of forest stands increases the probabilities of windthrow, snow breakage, and insect outbreak occurrences. Norway spruce or spruce dominated stands were often found to be more prone to wind, snow, and insect damage than some other conifer or broadleaf dominated stands (Nykänen et al., 1997; Mosandl and Felbermeier, 1999; Jalkanen and Mattila, 2000; Dobbertin, 2002, 2005; Wermelinger et al., 2002; Spiecker et al., 2004; Schütz, 2005; Hanewinkel et al., 2008; Knoke et al., 2008). Schütz et al. (2006) found that pure spruce stands were 2.7-3.8 times more vulnerable and damaged by windthrows than pure European beech stands. Similar results with even higher ratios were reported in Germany (Knoke et al., 2008). The admixture of up to 20 % of broadleaves in a stand lowers the susceptibility to windthrow by a factor of 3.4 (Schütz et al., 2006). However, we did not find any statistically significant relationship between the proportion of broadleaves in a stand and the occurrence of windthrow or insect outbreaks. But the results showed that even a small proportion of broadleaves in a stand significantly decreased the probability of snow breakage occurrence. In confirmation, Nykänen et al. (1997) reported that in general deciduous species are less susceptible to snow damage than conifers.

However, spruce is often one of the main tree species in uneven-aged forests in alpine forests (Ott et al., 1997), which were often reported to be more resistant to natural disturbances than even-aged forest stands (Dvorak et al., 2001; Dobbertin, 2002; Bachmann and Dvorak, 2005). However, Mason (2002) discussed that there is no major difference in resistance to wind between even-aged and uneven-aged stands; trees in uneven-aged stands are just more resistant to stem breakage due to a lower height/diameter ratio. A similar pattern was found by Dobbertin (2005) when investigating the consequences of the Lothar windthrow in even-aged and uneven-aged stands in Switzerland. Regarding snow damage, there is conflicting evidence on the influence of uneven-aged stand structure. Some claimed that in areas at high risk for snow damage, uneven-aged structures should be promoted since their benefits are derived from higher stem taper and even distribution of snow through the stand, but others suggested the promotion even-aged stands and evenly distributed and widely spaced trees (see in Nykänen et al., 1997).

Important impacts on natural disturbance occurrences were found to also have prior forest management activities and previous natural disturbances. Regeneration cuts, reflected in the proportions of regeneration and stand in rejuvenation in a compartment, create canopy gaps, thereby raising the length of the internal forest edge, which was often found to increase the susceptibility of stands to windthrows (e.g. Wraber, 1950; Ruel, 2000; Pellikka and Järvenpää, 2003; Ogris et al., 2004; Schütz, 2005; Schütz et al., 2006) and insect attacks (e.g. Peltonen, 1999; Gilbert et al., 2005); our results are consistent with this. On the contrary, the probabilities of snow breakage occurrence decreased with increasing proportions of regeneration and stand under rejuvenation. In the literature, there is an inconsistency regarding this issue since some argue that regeneration lowers the susceptibility of stands to snow damage while others negate this (see in Nykänen et al., 1997).

Similar to regeneration cuts, prior thinning activities within the previous 5 years caused higher susceptibility of stands to windthrows and snow breakages, but not to insect outbreaks. Thinning activities were often reported as a relevant independent variable when considering wind or snow damage (Jalkanen and Matilla, 2000; Cameron, 2002; Pellikka and Järvenpää, 2003; Dobbertin, 2005), but some studies also negated such a conclusion (e.g. Schütz et al., 2006).

As previously confirmed (Dobbertin, 2002, 2005; Schütz et al., 2006; Hanewinkel et al., 2008), previous natural disturbance occurrence in a compartment within the previous 5 years was found to significantly influence the occurrence of the analysed natural disturbances. But unexpectedly its association to insect outbreaks was negative, which means that the relative frequency of insect outbreak occurrence was lower in events when previous natural disturbance occurred than in events when it did not occur. Such a finding is contrary to the conclusions of most studies dealing with interactions among natural disturbances (Veblen et al., 1994; Wermelinger et al., 2002; Hanewinkel et al., 2008; Papler-Lampe and Kolšek, 2009).

Among site characteristics, several variables were related to natural disturbance occurrences, but most were related to snow breakage occurrence. Aspect was often reported as an important factor influencing the occurrence of natural disturbances. Considering that the main winds in the study area blow from the SW, W, and NW, the leeward sites were most frequently damaged. They were often subjected to substantial damage, presumably because of the wind turbulence effect behind the ridges (e.g. Schütz, 2005). Snow damage was also the most frequent on leeward sites (N, NE, and E) and sites on plane, which could be caused by wind depositing snow behind the ridges where wind cannot dislodge the snow load. In particular conditions, the interaction of snow load and at least moderate-intensity wind could lead to catastrophic disturbance events (Nykänen et al., 1997). Somewhat contrary to our expectations, the highest relative frequencies of insect outbreaks were not found only on warmer SE, S, SW, W aspects (Wermelinger, 2004), but also on NE and E aspects, which could be explained by the interaction between insect outbreaks and the other two disturbances, windthrows and snow breakages (Wermelinger et al., 2002; Dobbertin, 2005; Hanewinkel et al., 2008), which mainly occurred on these aspects. Elevation was also often reported as an important influential factor for windthrow, snow breakage, or insect outbreak occurrences (e.g. Jalkanen and Matilla, 2000; Wermelinger, 2004; Mayer et al., 2005; Evans et al., 2007; Seidl et al., 2007; Hanewinkel et al., 2008), but in our case it was only found as a predictor for snow breakage occurrence. Inclination was found to be a significant predictor only for snow breakage occurrence, not for windthrow as has sometimes been stated (e.g. Dobbertin, 2002; Mayer et al., 2005).

Besides the investigated variables, some other site and stand variables were stated to influence the natural disturbance occurrence. Wind and snow characteristics have a considerable impact on the occurrence of natural disturbances (e.g. Nykänen et al., 1997; Ruel, 2000; Schütz et al., 2006). Among stand characteristics, stand height, density, age, and mean diameter tree were found to influence windthrows (Wraber, 1950; Jalkanen and Matilla, 2000; Dobbertin, 2002, 2005; Mayer et al., 2005; Evans et al., 2007), while stand density and stand height significantly influenced snow damage (Nykänen et al., 1997; Pellikka and Järvenpää, 2003), and stand height and stand age influenced insect outbreaks (Wermelinger, 2004). Mainly windthrows (Wraber, 1950; Ruel, 2000; Dobbertin, 2002; Ogris et al., 2004; Mayer et al., 2005; Hanewinkel et al., 2008), but also insect outbreaks (Wermelinger, 2004), were found to be related to soil characteristics, such as soil type, depth, acidity, stone content, humus form, the content of soil nutrients, water supply, and permeability. Jalkanen and Matilla (2000) determined a minor influence of climate characteristics, such as temperature sum, on windthrow and snow damage occurrences, while bark beetle attacks were significantly influenced by temperature and precipitation (Seidl et al., 2007). However, in our study the data on climate variables were apparently not of sufficient quality and accuracy to be included in the analysis. The root rot in Norway spruce, associated with forest grazing (e.g. Wraber, 1950; Ogris et al., 2004) or decay due to other fungi infestations (e.g. Ruel, 2000), might have an impact on natural disturbance occurrence.

CONCLUSIONS WITH IMPLICATIONS FOR FOREST MANAGEMENT

The forest management regime was found to have a significant impact on the dynamics of forest stands in the studied forest type (Klopčič and Bončina, 2011). In addition, forest stand management can play a significant role in reducing the hazard and severity of natural disturbances (e.g. Gardiner and Quine, 2000). Since natural disturbances represent a significant impediment to regular forest management in the region, much can be done to improve the resistance of forest stands despite the stochastic nature of natural disturbance occurrences (Ruel, 2000; Kramer et al., 2001; Schütz et al., 2006).

Uneven-aged, irregular, multi-layered stand structure should be promoted over even-aged, regular, single-layered stand structures, especially in high-risk areas. Uneven-aged stand structure promotes a higher stem taper of trees (i.e. lower height/diameter ratio), which enhances the mechanical stability of trees and stands (Kotar, 2005). Considering the fact that the stand edge effect increases the susceptibility of stands to wind (e.g. Ruel, 2000; Pellikka and Järvenpää, 2003; Ogris et al., 2004) and insect (e.g. Peltonen, 1999; Gilbert et al., 2005) disturbances, small-scale group selection system, but mainly very small-scale irregular shelterwood ("der verfeinerte Femelschlag") silvicultural system, are suggested since they create horizontally fine-grained and vertically diverse forest structures with gradual transitions between forest stands of different developmental phases, stand heights, and ages. In limited areas "plentering" (single tree selection) could also be practiced, but site conditions and current stand structure would have to make it pertinent and feasible.

The mechanical stability and resistance of stands to natural disturbances can also be improved by thinning activities. It was found that thinning makes forest stands more prone to natural disturbances in the short-term, but in the long-term it improves the mechanical stability of trees and stands by promoting a higher stem taper and better anchorage of trees (König, 1995; Kotar, 2005; Schütz et al., 2006). It could be suggested that thinning activities should be carried out in the same manner as thinning from above, which has to be intensive enough in terms of early enough commencement and frequent repetition.

The already low admixture of broadleaves in coniferous-dominated stands significantly decreased their susceptibility to natural disturbance. Therefore, natural regeneration, favouring mixed tree species composition with noticeable proportions of broadleaves, but also other naturally present conifer species (e.g. fir, European larch (*Larix decidua* Mill.)), should be promoted. Tending and thinning silvicultural measures can further direct tree species composition of the regeneration towards a desired or at least acceptable composition with substantial admixture of deciduous species.

Since the analysed forests have been substantially altered in their structure and composition, and anthropogenic influences have continued to an ever-increasing extent, the question arose as to whether natural disturbances are still “natural”. They have more of a combined disturbance character (Anko, 1993) due to the coincidence of obvious anthropogenic impacts and the naturalness of the site and disturbance agents. The potential forest type at these sites is alpine silver fir-European beech forest with a substantially lower proportion of Norway spruce than the current forest has. The artificial spread of spruce’s distribution range to lowland sites and sites with unfavourable conditions, even on deforested and degradable sites (Spiecker et al., 2004), has already caused an increase in the severity of annual damage, but due to the ageing of stands, even greater damage is expected. Therefore, the suggested silvicultural measures and other close-to-nature silviculture principles should be promoted, at least in high-risk forest areas.

REFERENCES

Anko B. 1993. Vpliv motenj na gozdni ekosistem in na gospodarjenje z njim. Zbornik gozdarstva in lesarstva, 42: 85-109.

Attiwill P. M. 1994. The Disturbance of Forest Ecosystems - the Ecological Basis for Conservative Management. Forest Ecology and Management, 63, 2/3: 247-300.

Bachmann P., Dvorak L. 2005. Sturmschäden in Abhängigkeit vom Bestandesaufbau in einem Plenterwaldgebiet. V: LOTHAR Ursächliche Zussammenhänge und Risikoentwicklung. Synthese des Teilprogramms 6. Umwelt-Materialen Nr.184. M. Indermühle, P. Raetz and R. Volz (ur.). Bern, Swiss, Bundesamt für Umwelt, Wald und Landschaft: 51-59.

Bernik R. 1966. Katastrofe v gozdovih triglavskega gozdnogospodarskega območja. Gozdarski vestnik, 24: 270-273.

Bleiweis S. 1983. Pogostnost in obseg škod zaradi ujm v slovenskih gozdovih. Gozdarski vestnik, 41, 6: 233-249.

Bončina A. 2009. Urejanje gozdov - Upravljanje gozdnih ekosistemov. Ljubljana, Biotehniška fakulteta, Oddelek za gozdarstvo in obnovljive gozdne vire: 359 p.

Cameron A. D. 2002. Importance of early selective thinning in the development of long-term stand stability and improved log quality: a review. Forestry, 75, 1: 25-35.

Dale V. H., Joyce L. A., McNulty S., Neilson R. P., Ayres M. P., Flannigan M. D., Hanson P. J., Irland L. C., Lugo A. E., Peterson C. J., Simberloff D., Swanson F. J., Stocks B. J., Wotton B. M. 2001. Climate change and forest disturbances. Bioscience, 51, 9: 723-734.

Deanković T. 1969. Snegolomi v Julijskih Alpah in njihovi vzroki. Gozdarski vestnik, 27, 9: 223-236.

Diaci J., McConnell S. 1996. Sonaravno gospodarjenje z gozdovi in gospodarjenje z ekosistemi. Zbornik gozdarstva in lesarstva, 49: 105-127.

Dobbertin M. 2002. Influence of stand structure and site factors on wind damage comparing the storms Vivian and Lothar. Forest, Snow and Landscape Research, 77, 1/2: 187-205.

Dobbertin M. 2005. Erfassung der Bestandesdaten und Schäden auf dem repräsentativen 4×4-km Sanasilva-Netz. V: LOTHAR Ursächliche Zusammenhänge und Risikoentwicklung. Synthese des Teilprogramms 6. Umwelt-Materialien Nr. 184. M. Indermühle, P. Raetz, R. Volz (ur.). Bern, Bundesamt für Umwelt, Wald und Landschaft: 39-50.

Dorland C., Tol R. S. J., Palutikof J. P. 1999. Vulnerability of the Netherlands and northwest Europe to storm damage under climate change. Climatic Change, 43, 3: 513-535.

Dvorak L., Bachmann P., Mandallaz D. 2001. Sturmschäden in ungleichförmigen Beständen. Schweizerische Zeitung für Forstwessen, 152, 11: 445-452.

Evans A. M., Camp A. E., Tyrrell M. L., Riely C. C. 2007. Biotic and abiotic influences on wind disturbance in forests of NW Pennsylvania, USA. Forest Ecology and Management, 245, 1/3: 44-53.

Firm D., Nagel T. A., Diaci J. 2009. Disturbance history and dynamics of an old-growth mixed species mountain forest in the Slovenian Alps. Forest Ecology and Management, 257, 9: 1893-1901.

FMP Bled 2003. Forest Management Plan GGO Bled 2001-2010. Ljubljana, Slovenia Forest Service.

Frelich L. E. 2002. Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen-Deciduous Forests. Cambridge, Cambridge University Press: 266 p.

Fuhrer J., Beniston M., Fischlin A., Frei C., Goyette S., Jasper K., Pfister C. 2006. Climate risks and their impact on agriculture and forests in Switzerland. Climatic Change, 79, 1: 79-102.

Gardiner B. A., Quine C. P. 2000. Management of forests to reduce the risk of abiotic damage - a review with particular reference to the effects of strong winds. Forest Ecology and Management, 135: 261-277.

Genries A., Morin X., Chauchard S., Carcaillet C. 2009. The function of surface fires in the dynamics and structure of a formerly grazed old subalpine forest. Journal of Ecology, 97, 4: 728-741.

Gilbert M., Nageleisen L. M., Franklin A., Gregoire J. C. 2005. Post-storm surveys reveal large-scale spatial patterns and influences of site factors, forest structure and diversity in endemic bark-beetle populations. Landscape Ecology, 20, 1: 35-49.

Gill R. M. A. 1992. A review of damage by mammals in north temperate forests. 3. Impact on trees and forests. Forestry, 65, 4: 363-388.

Hanewinkel M., Breidenbach J., Neeff T., Kublin E. 2008. Seventy-seven years of natural disturbances in a mountain forest area — the influence of storm, snow, and insect damage analysed with a long-term time series. Canadian Journal of Forest Research, 38, 8: 2249-2261.

Hanewinkel M., Zhou W. C., Schill C. 2004. A neural network approach to identify forest stands susceptible to wind damage. Forest Ecology and Management, 196, 2-3: 227-243.

Jakša J., Kolšek M. 2010. Naravne ujme v slovenskih gozdovih. V: Naravne nesreče: od razumevanja do upravljanja. M. Zorn, B. Komac, M. Pavšek, P. Pagon (ur.). Ljubljana, Založba ZRC: 39-48.

Jalkanen A., Mattila U. 2000. Logistic regression models for wind and snow damage in northern Finland based on the National Forest Inventory data. Forest Ecology and Management, 135, 1/3: 315-330.

Johann E. 2007. Traditional forest management under the influence of science and industry: The story of the alpine cultural landscapes. Forest Ecology and Management, 249, 1/2: 54-62.

Kilpeläinen A., Gregow H., Strandman H., Kellomäki S., Venäläinen A., Peltola H. 2010. Impacts of climate change on the risk of snow-induced forest damage in Finland. Climatic Change, 99, 1: 193-209.

Klopčič M., Bončina A. 2011. Stand dynamics of silver fir (*Abies alba* Mill.)-European beech (*Fagus sylvatica* L.) forests during the past century: a decline of silver fir? Forestry, (in press).

Klopcic M., Poljanec A., Gartner A., Boncina A. 2009. Factors related to natural disturbances in mountain Norway spruce (*Picea abies*) forests in the Julian Alps. Ecoscience, 16, 1: 48-57.

Knoke T., Ammer C., Stimm B., Mosandl R. 2008. Admixing broadleaved to coniferous tree species: a review on yield, ecological stability and economics. European Journal of Forest Research, 127, 2: 89-101.

König A. 1995. Sturmgefährdung von Beständen im Alterklassenwald. Frankfurt am Main, J.D. Sauerländer's Verlag: 189 p.

Kotar M. 2005. Zgradba, rast in donos gozda na ekoloških in fizioloških osnovah. Ljubljana, Zveza gozdarskih društev Slovenije, Zavod za gozdove Slovenije: 500 p.

Kramer M. G., Hansen A. J., Taper M. L., Kissinger E. J. 2001. Abiotic controls on long-term windthrow disturbance and temperate rain forest dynamics in southeast Alaska. Ecology, 82, 10: 2749-2768.

Mason W. L. 2002. Are irregular stands more windfirm? Forestry, 75, 4: 347-355.

Mayer P., Brang P., Dobbertin M., Hallenbarter D., Renaud J.-P., Walthert L., Zimmermann S. 2005. Forest storm damage is more frequent on acidic soils. Annals of Forest Science, 62, 4: 303-311.

Mosandl R., Felbermeier B. 1999. Auf dem Weg zum naturnahen Wald. AFZ/Der Wald, 17: 910-914.

Nagel T. A., Levanič T., Diaci J. 2007. A dendroecological reconstruction of disturbance in an old-growth *Fagus-Abies* forest in Slovenia. Annals of Forest Science, 64, 8: 891-897.

Nilsson C., Stjernquist I., Barring L., Schlyter P., Jonsson A. M., Samuelsson H. 2004. Recorded storm damage in Swedish forests 1901-2000. Forest Ecology and Management, 199, 1: 165-173.

Nykänen M.-L., Peltola H., Quine C., Kellomäki S., Broadgate M. 1997. Factors affecting snow damage of trees with particular reference to European conditions. Silva Fennica, 31, 2: 193-213.

Ogris N., Džeroski S., Jurc M. 2004. Windthrow factors - a case study on Pokljuka. Zbornik gozdarstva in lesarstva, 74: 59-76.

Oliver C. D., Larsen B. C. 1996. Forest Stand Dynamics. New York, Wiley: 520 p.

Ott E., Frehner M., Frey H. U., Lüscher P. 1997. Gebirgsnadelwälder: Ein praxisorientirter Leitfaden für eine standortgerechte Waldbehandlung. Bern, Paul Haupt Verlag: 287 p.

Papler-Lampe V. 2008. Snegolom, ki je januarja 2007 prizadel blejske gozdove. Gozdarski vestnik, 66, 5/6: 309-319.

Papler-Lampe V., Kolšek M. 2009. Posledice snegoloma decembra 2008 v Gozdnogospodarskem območju Bled. Novice iz varstva gozdov, 2: 9-10.

Pellikka P., Järvenpää E. 2003. Forest stand characteristics and wind and snow induced forest damage in boreal forest. V: Proceedings of the International Conference on Wind Effects on Trees. B. Ruck (ur.). Karlsruhe, University of Karlsruhe: 269-276.

Peltonen M. 1999. Windthrows and dead-standing trees as bark beetle breeding material at forest-clearcut edge. Scandinavian Journal of Forest Research, 14, 6: 505-511.

Pickett S. T., White P. S. 1985. The Ecology of Natural Disturbance and Patch Dynamics. San Diego, Academic Press: 472 p.

Ruel J. C. 2000. Factors influencing windthrow in balsam fir forests: from landscape studies to individual tree studies. Forest Ecology and Management, 135, 1/3: 169-178.

Schelhaas M. J., Nabuurs G. J., Schuck A. 2003. Natural disturbances in the European forests in the 19th and 20th centuries. Global Change Biology, 9, 11: 1620-1633.

Schiesser H. H., Pfister C., Bader J. 1997. Winter storms in Switzerland North of the Alps 1864/1865–1993/1994. Theoretical and Applied Climatology, 58, 1: 1-19.

Schumacher S., Bugmann H. 2006. The relative importance of climatic effects, wildfires and management for future forest landscape dynamics in the Swiss Alps. Global Change Biology, 12, 8: 1435-1450.

Schütz J. P. 2005. Einfluss verschiedener Faktoren auf Art und Ausmass der Sturmschäden: Windcharacteristic und Sturmschäden im Raum Reusstal-Limattal. V: LOTHAR Ursächliche Zusammenhänge und Risikoentwicklung. Synthese des Teilprogramms 6. Umwelt-Materialien Nr. 184. M. Indermühle, P. Raetz, R. Volz (ur.). Bern, Bundesamt für Umwelt, Wald und Landschaft: 29-38.

Schutz J. P., Gotz M., Schmid W., Mandallaz D. 2006. Vulnerability of spruce (*Picea abies*) and beech (*Fagus sylvatica*) forest stands to storms and consequences for silviculture. European Journal of Forest Research, 125, 3: 291-302.

Seidl R., Baier P., Rammer W., Schopf A., Lexer M. J. 2007. Modelling tree mortality by bark beetle infestation in Norway spruce forests. Ecological Modelling, 206, 3/4: 383-399.

Spiecker H., Hansen J., Klimo E., Skovsgaard J. P., Sterba H., von Teuffel K. 2004. Norway Spruce Conversion - Options and Consequences. European Forest Institute, Joensuu, Finland: 269 p.

Splechtna B. E., Gratzer G., Black B. A. 2005. Disturbance history of a European old-growth mixed-species forest - A spatial dendro-ecological analysis. Journal of Vegetation Science, 16, 5: 511-522.

Stathers R. J., Rollerson T. P., Mitchell S. J. 1994. Windthrow Handbook for British Columbia Forests. Working Paper 9401. Victoria, British Columbia, BC Ministry of Forests.

Ulanova N. G. 2000. The effects of windthrow on forests at different spatial scales: a review. Forest Ecology and Management, 135, 1/3: 155-167.

Veber I. 1986. Gozdovi bohinjskih fužinarjev. Bled, Gozdno gospodarstvo Bled: 48 p.

Veblen T. T., Hadley K. S., Nel E. M., Kitzberger T., Marion R., Villalba R. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. Journal of Ecology, 82, 1: 125-135.

Wermelinger B. 2004. Ecology and management of the spruce bark beetle *Ips typographus* - a review of recent research. Forest Ecology and Management, 202, 1/3: 67-82.

Wermelinger B., Duelli P., Obrist M. K. 2002. Dynamics of saproxylic beetles (*Coleoptera*) in windthrow areas in alpine spruce forests. Forest, Snow and Landscape Research, 77, 1/2: 133-148.

Wick L., Mohl A. 2006. The mid-Holocene extinction of silver fir (*Abies alba*) in the Southern Alps: a consequence of forest fires? Palaeobotanical records and forest simulations. Vegetation History and Archaeobotany, 15, 4: 435-444.

Wraber M. 1950. O vzrokih in posledicah vetroloma na Jelovici. Gozdarski vestnik, 8: 306-309.

Zupančič M. 1969. Vetrolomi in snegolomi v Sloveniji v povojni dobi. Gozdarski vestnik, 27: 193-210.

2.4 FACTORS RELATED TO NATURAL DISTURBANCES IN MOUNTAIN NORWAY SPRUCE (*Picea abies*) DOMINATED FORESTS IN THE JULIAN ALPS

Klopčič M., Poljanec A., Gartner A., Bončina A. 2009. Factors related to natural disturbances in mountain Norway spruce (*Picea abies*) dominated forests in the Julian Alps. = [Vplivni dejavniki naravnih motenj v zasmrečenih gorskih gozdovih v Julijskih Alpah]. Ecoscience, 16, 1: 48-57

ÉCOSCIENCE
16 (1): 48-57 (2009)

Factors related to natural disturbances in mountain Norway spruce (*Picea abies*) forests in the Julian Alps[1]

Matija KLOPCIC & Ales POLJANEC, University of Ljubljana, Biotechnical Faculty, Department of Forestry and Renewable Forest Resources, Vecna pot 83, 1000 Ljubljana, Slovenia.
Andrej GARTNER, Slovenia Forest Service, Regional Unit Bled, Ljubljanska 19, 4260 Bled, Slovenia.
Andrej BONCINA[2], University of Ljubljana, Biotechnical Faculty, Department of Forestry and Renewable Forest Resources, Vecna pot 83, 1000 Ljubljana, Slovenia,
e-mail: andrej.boncina@bf.uni-lj.si

Abstract: An analysis of natural disturbances in the Julian Alps was carried out in the Jelovica-Pokljuka region (9627 ha) for the period 1979–2006. Data from salvage cuttings were used to examine the occurrence of windthrow, snow break, and insect attack disturbances in relation to site and stand characteristics, previous disturbances, and forest management. Forest stands at the site were characterized by a high growing stock (400 $m^3 \cdot ha^{-1}$ on average) and a large proportion of Norway spruce (87%). Salvage cutting due to windthrow, snow break and insect attacks was strongly related to altitude, aspect, topographic position, diameter structure, developmental phase of the stands, and forest landscape heterogeneity. Pole stands were more susceptible to snow breakage and less susceptible to windthrow and insect attack. A more heterogeneous forest landscape increased the risk of windthrow and insect attack occurrence, while the severity of all natural disturbances was lower in more heterogeneous forest landscapes. Natural disturbances and previous cuttings also significantly influenced the likelihood of occurrence and the severity of subsequent disturbances. To improve stand resistance, forest management measures considering the silviculture system and thinning are discussed.
Keywords: insect attack, intermediate natural disturbance, salvage cutting, snow breakage, stand resistance, windthrow.

Résumé : Une analyse des perturbations naturelles dans les Alpes Juliennes a été effectuée dans la région de Jelovica-Pokljuka (9627 ha) pour la période 1979-2006. Les données de coupes de récupération ont été utilisées pour examiner la fréquence des perturbations liées aux chablis, aux ruptures causées par la neige et aux épidémies d'insectes en fonction des caractéristiques du site et du peuplement, des perturbations précédentes et de l'aménagement forestier. Les peuplements forestiers du site étaient caractérisés par un volume de bois sur pied élevé (400 $m^3 \cdot ha^{-1}$ en moyenne) et une proportion importante d'épinette de Norvège (87 %). Les coupes de récupération dues aux chablis, aux ruptures causées par la neige et aux épidémies d'insectes étaient fortement liées à l'altitude, à l'aspect, à la position topographique, à la structure de diamètres, au stade de développement des peuplements et à l'hétérogénéité du paysage forestier. Les peuplements composés de perches étaient plus susceptibles aux ruptures causées par la neige et moins susceptibles aux épidémies d'insectes et aux chablis. Un paysage forestier plus hétérogène augmentait le risque de chablis et d'épidémie d'insectes, mais diminuait la sévérité de tous les types de perturbations naturelles. De précédentes perturbations naturelles et coupes de récupération influençaient significativement la probabilité et la sévérité des perturbations subséquentes. Afin d'améliorer la résistance des peuplements, des mesures d'aménagement forestier tenant compte du type de sylviculture et de l'utilisation de l'éclaircie sont discutées.
Mots-clés : chablis, coupe de récupération, épidémie d'insectes, perturbation naturelle intermédiaire, résistance du peuplement, rupture causée par la neige.

Nomenclature: Pfeffer, 1995; Oberdorfer, 2001.

Introduction

Natural disturbances are an integral component of forest ecosystems (Pickett & White, 1985; Attiwill 1994; Frelich, 2002) and have a strong influence on forest stand dynamics (*e.g.*, Ulanova, 2000; Woods, 2004; Nagel & Diaci, 2006). The effect of natural disturbances on stand dynamics varies between different forest types. In the mountain forests of Central Europe, which represent the majority of the total forest cover in the region (Brassel & Brändli, 1999; Boncina, Robic & Mikulic, 2001), wind, snow, and bark beetles are the main disturbance agents (Spiecker, 2000; Schelhaas, Nabuurs & Schuck, 2003). These forests have been important from an economic and protective point of view for centuries (Kräuchi, Brang & Schönenberger, 2000; Brang *et al.*, 2001). In many regions the tree species composition and stand structure of mountain forests have been substantially modified, which has led to lower resistance of these forests to natural disturbances or altered patterns of stand dynamics. As a result, the damage caused by natural disturbances can be much greater than in forests with natural composition and structure (Spiecker, 2000).

Knowledge of the natural disturbance regime is important for nature-based forest management; it enables an

[1]Rec. 2008-03-10; acc. 2008-09-15.
Associate Editor: Renzo Motta.
[2]Author for correspondence.
DOI 10.2980/16-1-3181

understanding of natural stand dynamics, which can then be mimicked in managed forests (Franklin, 1993; Diaci, 2006), and also minimizes the hazards and damage caused by disturbances in forest management (Gartner *et al.*, 2007). In mountain forests of Central Europe, the severity and frequency of natural disturbances vary greatly as a consequence of interactions between different disturbance agents, site characteristics, and stand properties (Brang, 2005). At one end of the spectrum, individual or small groups of snapped or uprooted trees create small gaps. These small-scale disturbances are usually very frequent, and gaps are often rapidly filled by lateral in-growth of existing canopy trees (Splechtna & Gratzer, 2005; Zeibig, Diaci & Wagner, 2005). However, gaps may also expand over time during subsequent disturbance events (Worrall, Lee & Harrington, 2005). At the other end of the spectrum, catastrophic disturbances can damage areas over ten to thousands of hectares, removing a substantial part of the canopy cover in some stands. Disturbances in this range of severity are very infrequent. The return interval of such events may often be more than a thousand years (Canham, Papaik & Latty, 2001). Examples of such events in Central Europe include the Lothar and Vivian storms, both of which were well studied (*e.g.*, Dobbertin, 2002; Brang, 2005; Mayer *et al.*, 2005). By contrast, intermediate disturbances are often undocumented (Seymour, White & deMaynadier, 2002). They can appear as patchy but severe canopy damage or as widely dispersed moderate damage (Woods, 2004). These events should occur less frequently than small-scale disturbances and much more frequently than catastrophic events. Furthermore, the effects of intermediate severity events are different than catastrophic events, as they tend to interact with tree species and size and remove more vulnerable individuals, as opposed to complete canopy removal. In the area of the Julian Alps, intermediate disturbances are the primary source of canopy damage and have an important influence on stand dynamics (FMP Bled, 2003).

Many studies have documented spatial variation of damage caused by individual disturbances with regard to the interaction of different disturbance agents and differential vulnerability of forests to natural disturbances due to stand structure, tree species composition, and site characteristics (*e.g.*, Kramer *et al.*, 2001; Lorimer & White, 2003; Nilsson *et al.*, 2004). Usually only a single disturbance agent is studied—mainly wind, which is the primary agent of canopy disturbance in mountain forests of Central Europe (*e.g.*, Dobbertin, 2002; Mayer *et al.*, 2005). Several studies have shown that the frequency or spatial severity of intermediate disturbances are related to site and stand characteristics (*e.g.*, Mayer *et al.*, 2005; Nagel & Diaci, 2006). Some studies have also examined risk assessment through different methodological approaches (*e.g.*, Valinger & Fridman, 1997; Jalkanen & Matilla, 2000; Hanewinkel, Zhou & Schill, 2004; Hanewinkel *et al.*, 2008). However, there have been few attempts to examine the interaction of different disturbance agents on the formation of intermediate-scale disturbances in Europe (*e.g.*, Hanewinkel *et al.*, 2008).

The aim of this study was to analyze the most important natural disturbances—snow break, windthrow, and insect attack—and their interactions in the forest area of the Julian Alps, Slovenia. The primary objective was to determine the factors that might increase susceptibility to intermediate disturbances. Thus, the occurrence and severity of the 3 disturbance types were studied in regard to the following 3 groups of factors: 1) site characteristics; 2) stand characteristics; and 3) past human and natural disturbances. Additionally, we examined the following hypotheses: 1) even-aged stands and older stands are less wind-firm than uneven-aged and younger stands; 2) pole stands are the most susceptible to snow damage; and 3) management measures carried out in previous years and/or past natural disturbances reduce the resistance of stands against subsequent disturbances.

Methods

Study area

The Julian Alps lie in the northwestern part of Slovenia, at the southeastern end of the Alps. In spite of a long tradition of regular and nature-based forest management in the region, a large portion of forests were significantly changed as silvicultural practices more than century ago favoured Norway spruce (Johann, 2006), resulting in current spruce-dominated even-aged stands. These forests contain the spruce with the highest wood quality in Slovenia, as well as resonant wood, and are therefore very important from an economic standpoint. Additionally, the forests of the Julian Alps region are part of Triglav National Park and play important protective, habitat, and social functions. Forest damage caused by natural disturbance is common in the region and is the main threat to regular forest management (FMP Bled, 2003).

The research was carried out in the Pokljuka-Jelovica district (46° 20' N, 14° 00' E), which consists of 2 spatially dislocated though ecologically similar units totalling 9627 ha (Figure 1). It is further divided into 455 compartments with an average area of approximately 21 ha. Elevation ranges from 460 to 2010 m, and averages 1270 m. The prevalent parent materials are limestone and dolomite. The climate is characterized by a mean temperature of 3.8 °C and average annual precipitation of about 2000 mm. The vegetation period lasts 110–160 d, and the duration of snow cover averages about 160 d. The prevailing winds are

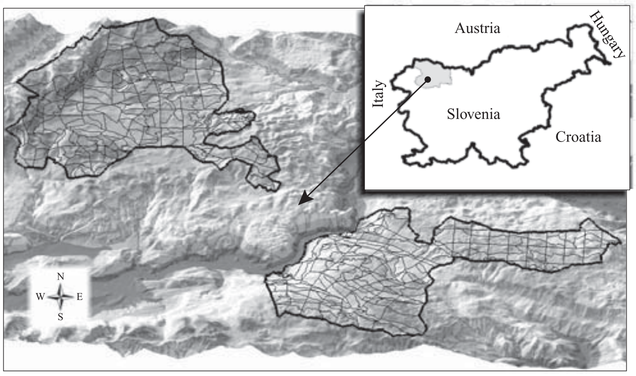

FIGURE 1. Position of the study area within Slovenia (inset) and the Pokljuka-Jelovica district (bold line) and compartments (thin line) shown on the digital elevation model.

from south-west, west, and north-west, reaching 50 m·s^{-1} (Gregorcic, Gregorcic & Bertalanic, 2002).

Based on the site conditions, the potential vegetation of this site should be dominated by silver fir (*Abies alba*) and European beech (*Fagus sylvatica*), classified as an *Abieti–Fagetum* association. However, the existing vegetation is classified as subalpine and montane spruce and montane mixed spruce–silver fir forest according to the European classification scheme (EEA, 2006). The site is characterized by a high growing stock (400 m^3·ha^{-1} on average) and even-aged forest stands, dominated by Norway spruce (87%), but silver fir (*Abies alba*), European beech (*Fagus sylvatica*), and sycamore (*Acer pseudoplatanus*) are also present.

DATA ACQUISITION AND DATABASE CREATION

This study is based on data from salvage cutting, which is defined as the removal of trees damaged or dying due to disturbance agents with the aim of recovering the value that would otherwise be lost. Single-tree-based silviculture has been practised in the study area, meaning that each tree intended for harvest is measured and recorded (Slovenia Forest Service, 2007). Salvage cutting is one of the cutting types; thus, the type, amount, structure, and temporal distribution of salvage cuttings can be used as an indicator of the natural disturbance regime in the region.

Data from all cut trees in the period 1979–2006 were analyzed. For each cut tree the following data were available: year of cutting, location (compartment), tree species, 5-cm-dbh class, and type of cutting (regular, salvage); salvage cuttings were further divided into 4 disturbance agent categories: windthrow, snow breakage, insect attack, and other. In the 28-y time period, 2 087 299 cut trees totalling 1 447 867 m^3 were recorded.

An inventory of forest stands is made every 10 y. It is based on a combination of a field survey of forest stands and permanent sampling plots (located on a 200- × 200-m grid; plot area = 400 m^2; *n* plots = 3470), where trees above 10 cm in dbh are measured. A GIS database for the Pokljuka-Jelovica district was constructed. It included the annual status of forest stands and the amount of salvage cutting per compartment. The value of the growing stock was updated for each year during the 10-y period considering the amount of the annual cut and annual volume increment of stands. Each row of the database represented an event. Thus, the database consisted of 12 740 (28 y × 455 compartments) rows (events) and 23 columns (variables).

In our analysis, the independent variables describe various site and stand conditions and past disturbance events in the compartments (Table I). The following stand variables were computed from the data derived from forest inventory records: the growing stock (m^3·ha^{-1}), categorized into small- (10 cm ≤ dbh < 30 cm), medium- (30 cm ≤ dbh < 50 cm) and large-diameter (50 cm ≤ dbh) trees; the proportion of Norway spruce and of broadleaved species (% of growing stock); and the proportions of the developmental phases in the total area of a compartment. The Shannon–Wiener index H' was used to examine forest landscape heterogeneity in the compartment (Pielou, 1975), calculated with Equation [1] using the relative abundance (p_i) of developmental phases in the total area of a compartment.

$$H' = -\sum_{i=1}^{m}(p_i \cdot ln\ p_i) \qquad [1]$$

Variables concerning site conditions were derived mainly from a digital elevation model (DEM) with a spatial resolution of 25 m and an average height accuracy of 1.5–6.5 m. The mean inclination and inclination standard deviation and the mean elevation and elevation standard deviation of the specific compartment were computed from the DEM, while mean aspect was recorded with 9 directions but was later

TABLE I. Variables used for modelling the occurrence and severity of natural disturbances.

	Variable	Variable type	Description of the variable	Candidates for modelling[a]
Site-characteristic variables	INC	continuous	Inclination (°)	–
	INC_STD	continuous	Standard deviation of inclination within the compartment	–
	ELV	continuous	Mean elevation of the compartment (m asl / 100 m)	included
	ELV_STD	continuous	Standard deviation of elevation within the compartment	included
	ASP	0 / 1	Aspect (1 = N+NE+E+SE; 0 = S+SW+W+NW)	included
	ASP_VAR	continuous	Variation of aspect within the compartment	–
	TOP	0 / 1	Topographic position (1 = ridge or hilltop; 0 = other)	included
	STO	continuous	Stoniness	–
	ROC	continuous	Rockiness	–
Stand-characteristic variables	VOL_A	continuous	Volume of small-diameter trees (dbh < 30 cm)	included
	VOL_B	continuous	Volume of medium-diameter trees (30 ≤ dbh < 50 cm)	included
	VOL_C	continuous	Volume of large-diameter trees (dbh ≥ 50 cm)	–
	H'	continuous	Forest landscape heterogeneity index (Shannon–Wiener index)	included
	Y_GR	continuous	Proportion of young growth and unrejuvenated gaps in the compartment	included
	PO_ST	continuous	Proportion of pole stands in the compartment	–
	MT_ST	continuous	Proportion of mature stands in the compartment	–
	RG_ST	continuous	Proportion of regeneration stands in the compartment	included
	UE_ST	continuous	Proportion of uneven-aged stands in the compartment	included
	SH_ST	continuous	Proportion of shrub and dwarf pine stands in the compartment	included
	P_SP	continuous	Proportion of Norway spruce in the compartment	–
	P_BR	continuous	Proportion of broadleaves in the compartment	–
Past events	PR_DS	0 / 1	Natural disturbance occurrence within previous 5 y (1 = yes; 0 = no)	included
	PR_CT	0 / 1	Presence of regular cutting within previous 5 y (1 = yes; 0 = no)	included

[a] –Indicates variables that were candidates for the multivariable model and were included in the stepwise procedure of logistic and linear regression modelling.

categorized into a dichotomous (0 / 1) variable (Table I). The topography variable (TOP) was recorded as the prevalent type of topographic position and later coded as a dichotomous (0 / 1) variable. Rock cover and bedrock cover were assessed visually by a terrestrial survey as the percentage of total surface covered by stones and rocks, respectively.

The disturbance index (DI), calculated as the ratio between the amount of salvage cutting and the total growing stock of the stands in the compartment, was used as an indicator of the disturbance severity and at the same time the criterion to define whether a disturbance occurred. The following 3 indices were calculated per compartment for each year: DIW, windthrow index; DIS, snow breakage index; and DII, insect attack index.

Dichotomous variables concerning disturbance occurrences within compartments for each year of the studied period were calculated. The threshold to determine if a natural disturbance has occurred is always somewhat arbitrary (Hanewinkel, Zhou & Schill, 2004); a different threshold of natural disturbance occurrence would result in a different model. In our case, a DI of 1% was adopted as a threshold, such that a natural disturbance caused by a particular agent occurred if the DI was equal to or larger than 0.01 (0 = a disturbance did not occur; 1 = a disturbance occurred). This threshold allowed us to exclude small-scale disturbances where only a single tree or a small group of trees were damaged or killed.

To assess if previous natural disturbance or regular cutting had an effect on subsequent disturbances, two dichotomous variables regarding events in a compartment in the last 5 y were added to the independent variables: the occurrence of disturbance(s) in any of the 5 previous years with severity larger than or equal to 1% of present growing stock (PR_DS) and the occurrence of a regular cut in the same period (PR_CT).

Data processing

The effects of various factors on natural disturbances on a compartment level were investigated with 2 different multiple regression approaches. A binary logistic regression (Hosmer & Lemeshow, 2000) was used to examine which variables predict the occurrence of natural disturbances. Therefore, a logit transformation was used to make the probability function behave linearly. Predicted probabilities (p) were calculated back to the original scale using Equation [2]:

$$p = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + ... + \beta_n x_n)}{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + ... + \beta_n x_n)} \qquad [2]$$

Predicted probabilities are the base for calculating the odds of an event occurring, which is defined as the ratio between the probability that the event occurs and the probability that the event fails to occur. Furthermore, the odds ratio can be calculated as the quotient between the odds of exposed and unexposed individuals. If the predicted probabilities are low among unexposed and exposed objects the odds ratio is appropriate for estimating the relative risk (Hosmer & Lemeshow, 2000).

An extensive set of 23 predictor variables classified as continuous or nominal (dichotomous) was analyzed to detect multi-collinearity and to gain a set of candidate variables for the modelling procedure (Guisian & Zimmermann, 2000; Hosmer & Lemeshow, 2000). Therefore, Pearson correlation coefficients (r) between continuous predictor variables were calculated, and only 1 variable of those pairs with $r > 0.45$ was accepted as the candidate to be included in the model. Next, contingency tables with χ^2-tests (for nominal variables) and 2-sample t-tests (for continuous variables) between the independent variable and all predictor variables were applied. Any variable whose univariable test had a P-value < 0.25 was accepted as a candidate for the multivariable model, while all other variables were excluded from the procedure. When the model was chosen, the variance inflation factor (VIF) of the predictor variables included in the model, calculated as $1/(1 - R^2)$, was compared to the critical value of 10 (Allison, 1999). R^2 was obtained in a linear regression (for continuous predictors) or in a logistic regression (for nominal variables) using one of the predictor variables as an independent variable and all others as dependent variables.

A selected set of predictor variables (Table I) was included in the forward stepwise logistic regression modelling procedure. The procedure was performed in SPSS 15.0 for Windows based on the maximum likelihood criterion with a maximum iteration number of 30. Goodness-of-fit was tested with the Hosmer–Lemeshow goodness-of-fit test (Hosmer & Lemeshow, 2000) and also with the estimated D^2 (Guisian & Zimmermann, 2000), which is calculated according to Equation [3]:

$$D^2 = (\text{null deviance} - \text{residual deviance}) / \text{null deviance} \qquad [3]$$

Standard multivariate linear regression was applied to model the severity of a particular disturbance type. The logarithmic transformation of the disturbance index DI as an indicator of disturbance severity in a compartment was used as an independent variable. Predictor variables included in the forward stepwise modelling procedure were the same as for the logistic regression (Table I).

To examine the differences between salvage-cut trees following windthrow, snow break, and insect attack, a Kruskal–Wallis ANOVA by ranks was used; 1 062 527 salvage-cut trees were included in the analysis. Post hoc tests of differences between the disturbance types were done using multiple comparisons of mean ranks for groups.

Results

Factors related to occurrence of natural disturbances

During the 1979–2006 study period, 1682 natural disturbances were registered among 12 740 events. Windthrows were the most frequent disturbance type, with 5.8% (n = 748 disturbances) of all events; they were more frequent than snow breakages (4.4%, n = 562) and insect attacks, which were mainly caused by *Ips typographus* and *Pytiogenes chalcographus* (3.5%, n = 451). Disturbances were most frequently categorized in the damage class of 1–5% of the total growing stock of forests in a compartment (628, 472, and 437 events for windthrow, snow break, and insect attacks, respectively). Eighteen windthrows out of 748 damaged

20% or more of the total growing stock, while only 1 snow breakage and no insect attacks were recorded in this DI class. However, in the majority of events the disturbance index was 0 (10 442, 11 459, and 11 295 for windthrow, snow break, and insect attacks, respectively) or the analyzed disturbance agents affected the stands with a severity lower than 1% of the total growing stock (1550, 719, and 994 for windthrow, snow break, and insect attacks, respectively).

Among the 13 variables (Table I) selected for the multivariate logistic analysis, 9 variables were included in the model for windthrow, 7 for snow breakage, and 7 for the insect attacks model (Table II). All variables were significant according to the Wald test ($P < 0.05$). The variance inflation factors (VIF) did not exceed the critical value of 10; therefore, all variables were kept in the model. The Hosmer–Lemeshow test showed that data fit the model well because of non-significant chi-square values (Table II). Goodness-of-fit for each of the 3 models was assessed by D^2; the snow disturbance model had the lowest D^2 value (0.04), while the values for the wind and insect attack model were only slightly higher: 0.09 and 0.14, respectively.

In the wind disturbance model only 1 site variable was included: susceptibility to wind disturbance was 1.24 times higher on the lee side of hills (N, NE, E, and SE aspects) compared to sites on a windward side of the hills (S, SW, W, and NW aspects). Among the tested stand variables, standing volume of small-diameter trees (VOL_A) lowered the risk of wind damage, while standing volume of medium-diameter trees (VOL_B) slightly increased it. A 100 $m^3 \cdot ha^{-1}$ increase of VOL_A reduced the risk of windthrow by a ratio of 0.44, while a 100 $m^3 \cdot ha^{-1}$ increase of VOL_B increased the risk by a ratio of 1.18. Among the stand variables, the largest differences in the odds ratio were related to H', where a more heterogeneous forest landscape increased the risk of wind disturbance. In the compartments with a higher proportion of uneven-aged stands and regeneration stands in the total area, the risk of windthrow was lower, while in stands with a higher proportion of young growth and gaps, the risk increased. Windthrows were 1.56 times more likely to occur in the compartments where regular cuttings (PR_CT) were carried out in the previous 5 y and 1.92 times more likely in the compartments where natural disturbance (PR_DS) had occurred in the same period compared to compartments with no disturbances in last 5 y.

In the snow disturbance model 2 site variables were included. An increase of elevation (ELV) reduced the risk of snow disturbance by a ratio of 0.90 for every 100 m in elevation change. Topographic diversity (ELV_STD) slightly reduced the risk of snow disturbance as well. Stands with a larger volume of small-diameter trees (VOL_A) were more susceptible to snow disturbances; a 100 $m^3 \cdot ha^{-1}$ increase of VOL_A increased the risk of snow disturbance by a ratio of 1.18. In the compartments with a higher proportion of uneven-aged stands, regeneration stands, gaps, and young growth in the total area, the risks of snow disturbances were lower. The model indicated that snow disturbances were 1.35 times more likely to occur in the compartments where regular cuttings (PR_CT) were carried out in the previous 5 y than in other compartments.

In the model for insect attacks 3 site variables were included. If explained as a relative risk, insect attacks would be 1.38 times more frequent in sites where aspect was coded as 0 (S, SW, W, NW) compared to stands on more shady sites (N, NE, E, and SE aspect) and 1.90 times more frequent on ridges and hilltops compared to the other topographic positions. Higher elevation reduced the risk of insect attacks by a ratio of 0.80 for every 100 m. Among the tested stand variables, standing volume of small-diameter trees (VOL_A) and Shannon–Wiener index H' were included in the model. A 100 $m^3 \cdot ha^{-1}$ increase of VOL_A reduced the risk of insect attack by a ratio of 0.44. A more heterogeneous forest landscape structure increased susceptibility to insect attacks. As expected, the model predicted that insect attacks would be 2.54 times more frequent in the compartments where natural disturbance(s) (PR_DS) occurred in the previous 5 y and 1.63 times more frequent where regular cuttings (PR_CT) were carried out in the same period, if compared to other compartments.

THE SEVERITY OF NATURAL DISTURBANCES

The severity of natural disturbances in the compartments was assessed by the disturbance index DI. Among the

TABLE II. Results of the binary logistic regression for prediction of natural disturbance occurrence (only predictors significant in at least 1 model are shown).

	Windthrow			Snow breakage			Insect attack		
Predictor variables	β	*P*	Exp(B)	β	*P*	Exp(B)	β	*P*	Exp(B)
Constant	–3.443	0.000	0.032	–1.739	0.001	0.176	–1.929	0.000	0.145
Y_GR	0.007	0.024	1.007	–0.011	0.001	0.989			
RG_ST	–0.007	0.027	0.993	–0.010	0.013	0.990			
UN_ST	–0.012	0.000	0.988	–0.018	0.000	0.983			
H'	0.449	0.000	1.566				1.497	0.000	4.470
VOL_A	–0.008	0.000	0.992	0.002	0.004	1.002	–0.008	0.000	0.992
VOL_B	0.002	0.003	1.002						
ELV				–0.104	0.007	0.901	–0.221	0.000	0.801
ELV_STD				–0.007	0.047	0.993			
TOP							0.644	0.000	1.903
ASP	0.214	0.046	1.239				–0.322	0.010	0.725
PR_DS	0.653	0.000	1.922				0.930	0.000	2.535
PR_CT	0.447	0.000	1.564	0.303	0.002	1.354	0.489	0.000	1.631
Hosmer–Lemeshow test		0.136			0.441			0.529	
D^2		0.087			0.037			0.141	

13 variables (Table I) selected for the multivariate analyses, 8 variables were included in the windthrow model, 9 in the snow breakage model, and 8 in the insect attack model (Table III). Multiple linear models showed weak relationships, with the highest R-square of 0.25 for the insect attack model (Table III).

Three site variables were included in the windthrow model. More severe damage caused by wind was observed on ridges and hilltops (TOP), while there was lower severity damage on topographically diverse terrain (ELV_STD). Elevation (ELV) was observed to have a minor although still significant influence on the DIW. A lower DIW was observed in the compartments with a large volume of small- (VOL_A) and medium-diameter trees (VOL_B) and in compartments with a more heterogeneous forest landscape (*H′*). However, more damage was observed in compartments with a high proportion of gaps and young growth and where previous natural disturbances within the past 5 y were recorded.

The snow breakage index DIS was larger for sites on the lee side of hills (N, NE, E, and SE aspects). Similar to the windthrow index, severity was higher on higher elevations and on ridges and hilltops, while it was lower on topographically diverse terrain (ELV_STD). DIS was also smaller if the proportion of medium-diameter trees (VOL_B) was high; VOL_A was not included in the model. A more heterogeneous forest landscape and compartments with a larger proportion of uneven-aged stands were less damaged, while DIS was lower if at least 1 (human or natural) disturbance occurred in the previous 5 y.

The insect attack index DII was larger for compartments on ridges and hilltops and with a large proportion of unrejuvenated gaps and young growth, while it was lower in sites with a higher topographic diversity (ELV_STD). As expected, the elevation variable was significant in the insect attack model, although it had only a small influence. DII was lower in compartments with a high standing volume of small- (VOL_A) and medium-diameter trees (VOL_B) and in compartments with a more heterogeneous forest landscape. Compartments with at least 1 recorded natural disturbance within the previous 5 y were more damaged by insect attacks.

Comparison of dbh of salvage-cut trees

Non-parametric analyses of salvage-cut trees (*n* = 1 062 527) in the period 1979–2006 showed significant differences in the mean dbh of trees damaged by snow, wind, and insects (Kruskal–Wallis, H = 24 959.90, *P* = 0.000). The median dbh of salvage-cut trees following snow break was the lowest, amounting to 17.5 cm (*n* = 625 395) (Figure 2), which corresponds to a dbh of trees in pole stands. Windthrows and insect attacks damaged larger trees, with a median dbh of 32.5 cm (*n* = 309 063) and 32.5 cm (*n* = 128 069), respectively (Figure 2), which correspond to the dbh of trees in the early mature developmental phase.

Discussion

Factors related to occurrence and severity of natural disturbances

In Europe, 35 million m^3 of timber per year are harvested because of natural disturbances, mainly from storm damage in the sub-Atlantic, Alpine, and Central Panonic zone, and mostly in mountainous areas (Schelhaas, Nabuurs & Schuck, 2003). One of the primary factors that has contributed to the increased severity of forest damage is conifer-oriented forest management (Spiecker, 2000), which has also been practised in the Slovene Julian Alps. In the Jelovica-Pokljuka district, the amount of salvage cutting during the last 28 y exceeded 43% of the total cut, mostly due to damage caused by wind (19%), snow (11%), and insects (7%). The remaining 6% was caused by other disturbance agents, including pollution, fir die-back, fungi, and diseases (Gartner *et al.*, 2007). A similar amount of salvage cutting due to the impact of wind and snow was reported by Hanewinkel *et al.* (2004) for the period 1980–1994 in the northern Black Forest, Germany.

In our study area the most severe disturbance was the snow breakage of 1961, which resulted in 128 000 m^3 of salvage-cut trees. The most severe windthrow occurred in 2006, damaging 72 000 m^3 of timber. Such catastrophic events are a result of unique climatic conditions and are often chaotic in nature (Canham, Papaik & Latty, 2001; Frelich, 2002; Ogris, Dzerovski & Jurc, 2004). These events occur very infrequently in most forest ecosystems (Lorimer

TABLE III. Fitted coefficients of multiple linear regression models for the severity of natural disturbance using a logarithmic transformation of the disturbance index (DI) as a dependent variable (only predictors significant in at least 1 model are shown).

Predictor variables	Windthrow			Snow breakage			Insect attack		
	β	SE	*P*	β	SE	*P*	β	SE	*P*
Constant	–1.421	0.170	0.000	–2.500	0.219	0.000	–0.767	0.160	0.000
Y_GR	0.004	0.001	0.001				0.002	0.001	0.039
UN_ST				–0.004	0.001	0.000			
H′	–0.199	0.042	0.000	–0.432	0.052	0.000	–0.191	0.043	0.000
VOL_A	–0.001	0.000	0.000				–0.002	0.000	0.000
VOL_B	–0.001	0.000	0.000	–0.002	0.000	0.000	–0.002	0.000	0.000
ELV	0.000	0.000	0.000	0.001	0.000	0.000	–0.001	0.000	0.000
ELV_STD	–0.003	0.001	0.001	–0.005	0.001	0.000	–0.004	0.001	0.000
TOP	0.099	0.031	0.001	0.159	0.046	0.001	0.156	0.027	0.000
ASP				0.276	0.049	0.000			
PR_DS	0.064	0.026	0.013	–0.112	0.037	0.003	0.078	0.025	0.002
PR_CT				–0.093	0.042	0.027			
R-Square	0.072			0.151			0.252		

& White, 2003; Nilsson *et al.*, 2004), including, it seems, in our study area. On the other hand, intermediate-severity disturbances occur more often (Woods, 2004). Such events were present each year during the studied period; the most common of these were windthrow events. In general, their occurrence depends on the interaction of several factors, including climatological and orographical factors, as well as forest stand characteristics and past silvicultural treatments (*e.g.*, Gardiner & Quine, 2000; Ruel, 2000; Kramer *et al.*, 2001; Frelich, 2002; Dobbertin, 2005).

Our study showed that among stand characteristics, site conditions, and past disturbances, the last ones were strongly related to the occurrence and severity of natural disturbances. Regular cutting in the previous 5 y significantly increased the susceptibility of stands to the occurrence of all 3 analyzed types of natural disturbances, a result that is in accordance with many other observations (*e.g.*, Dobbertin, 2005). However, multiple linear regression showed that regular cutting had no significant influence on salvage cutting caused by wind and insects, while the severity of snow breakage was even lower if regular cutting was done in the previous 5 y. Other studies have reported greater wind damage in stands where regular cutting was done at least once in the previous 5 y (Stathers, Rollerson & Mitchell, 1994; Dobbertin, 2005). In our study univariate analyses (2-sample *t*-test; results not shown) also indicated that damage caused by wind and snow was significantly larger in compartments where regular cutting was done in the previous 5 y, but this was not the case in the multiple linear model.

Forest stands previously damaged by disturbances are often more prone to subsequent disturbances than non-disturbed stands (König, 1995; Jalkanen & Mattila, 2000; Dobbertin, 2005). In our study, disturbances in the previous 5 y strongly increased the susceptibility of stands to windthrow and insect attacks, which could be a consequence of canopy gap formation during the disturbance and a greater amount of dead wood after the disturbance (Ogris, Dzerovski & Jurc, 2004). Additionally, we found a significant correlation (results not shown) between the amount of salvage-cut trees following snow breakages and windthrows and the amount of salvage-cut trees due to insects 2 y after snow breakages or windthrows had occurred. Similar findings were reported by Wermelinger, Duelli, and Obrist (2002). Past disturbances were not included as a predictor variable in the model for snow breakage occurrence, while multiple linear regression showed that past disturbances even decreased the severity of snow breakages.

Particular site variables were also significantly related to natural disturbances. We determined that sites with N, NE, E, and SE aspects were more susceptible to windthrow compared to those with other aspects (S, SW, W, and NW). In the study area, wind comes mainly from the SW, W, and NW; therefore, turbulence related to wind-flow on the lee side of the hills could be the main reason for wind damage. Numerous authors have stated that the intensity of the turbulence effect should be greatest in the area 2 to 3 tree heights behind the edge (*e.g.*, Schütz, 2005). Other studies (*e.g.*, Bachmann & Dvorak, 2005) found the opposite in uneven-aged forests, where stand damage due to windthrow

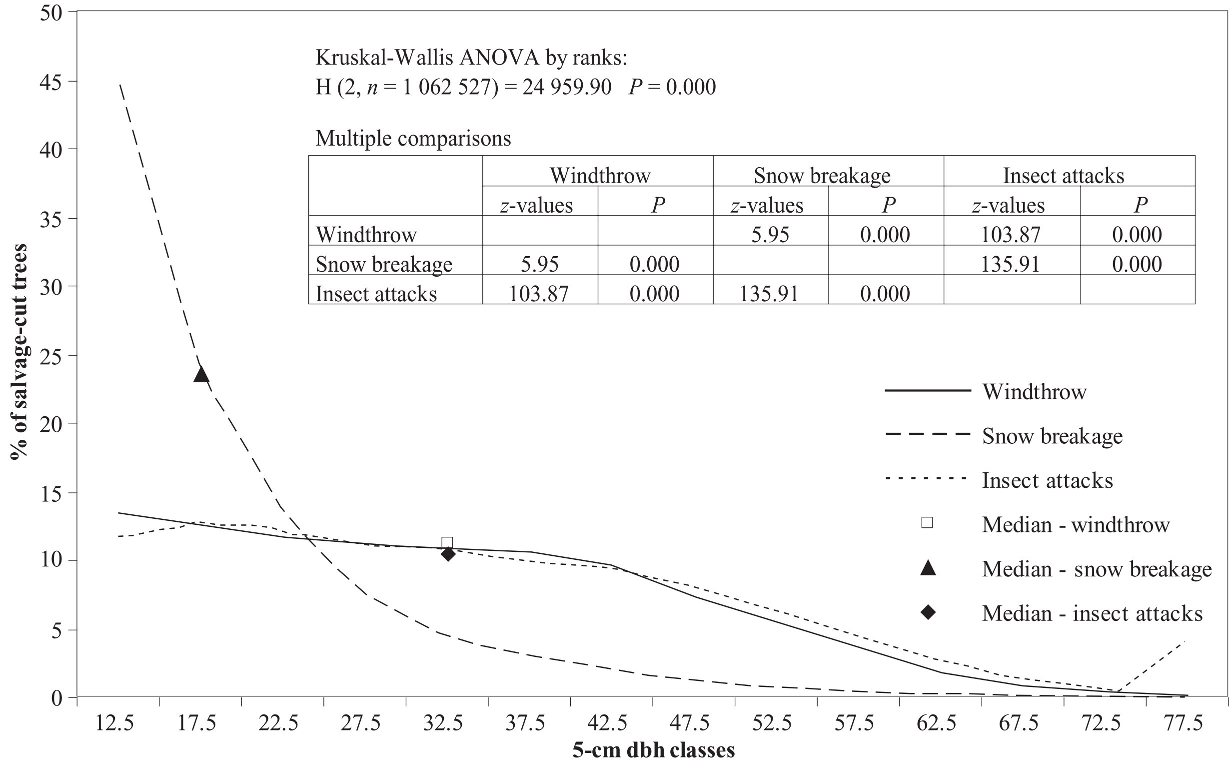

FIGURE 2. Distribution of relative frequencies of salvage-cut trees caused by natural disturbance agents per 5-cm-dbh class, with the results of the Kruskall–Wallis ANOVA by ranks and post hoc tests of multiple comparisons of mean ranks for groups.

was much lower on the lee side of the hills if compared to the wind-exposed side. Snow breakage was also more frequent on lee sites, which could be a consequence of prevailing winds depositing snow on the lee side of the ridges. As expected, the S, SW, W, and NW aspects significantly increased the risk of insect attack disturbances due to a greater heat influx on sun-exposed aspects.

Higher elevation reduced the risk of snow disturbances and insect attacks. On the other hand, the severity of windthrows and snow breakages was higher in higher elevations, although the linkage was very weak. Brang (2005) obtained similar results following the Lothar and Martin windthrows in Central Europe.

Topographic position seems to have an important influence on disturbance occurrence, but the relationships are not completely clear (Stathers, Rollerson & Mitchell, 1994). In our case, linear regression models showed that severity of all 3 types of natural disturbance was significantly higher on ridges and hilltops if compared to other topographic positions. Many studies have reported that stands growing on flats or slopes of smaller inclination are often more prone to windthrow (Brang, 2005; Bachmann & Dvorak, 2005). In our case, the inclination variable was not included in the multivariate analyses because of high correlation with topographic diversity (ELV_STD) ($r = 0.79$, linear regression: $P = 0.000$). The severity of all 3 types of disturbances was significantly lower in sites with a high ELV_STD value, which is in accordance with other observations (Stathers, Rollerson & Mitchell, 1994; Ruel, 2000; Schütz *et al.*, 2006).

Many stand variables were significantly associated with the occurrence of natural disturbances. The occurrence of windthrow disturbances was significantly positively related to the volume of medium-diameter trees (30 cm < dbh ≤ 50 cm), while the odds decreased significantly with an increasing volume of small-diameter trees (< 30 cm in dbh). The volume of large-diameter trees (VOL_C) and the proportion of pole stands (PO_ST) were not included in the multivariate analyses because of high correlation with the variable of small-diameter trees (VOL_A) ($r = -0.62$, linear regression: $P = 0.000$; and $r = 0.73$, linear regression: $P = 0.000$, respectively), while proportion of mature stands (MT_ST) was not included because of high correlation with the volume of medium-diameter trees (VOL_B) ($r = 0.68$, linear regression: $P = 0.000$). These findings suggest that windthrow disturbances would more likely occur in mature stands compared to younger stands. Additionally, the median dbh of salvage-cut trees due to windthrows was 32.5 cm, which was significantly larger than the median dbh of salvage-cut trees due to snow breakage, which was 17.5 cm. These results correspond to the assessment that stand age (Jalkanen & Mattila, 2000; Ruel, 2000) and stand height (König, 1995; Dobbertin, 2002) increase windthrow risk.

The presence of unrejuvenated gaps and young growth (Y_GR) was found to increase susceptibility to wind damage, while a higher proportion of uneven-aged and regeneration stands decreased the risk of windthrow. Our results were partly in accordance with other observations, as some researchers found regeneration with many canopy gaps to be often the most vulnerable developmental phase to windthrow (Ogris, Dzerovski & Jurc, 2004; Worrall, Lee & Harrington, 2005). A more heterogeneous forest landscape increased the susceptibility to windthrow disturbances of smaller intensity, since the severity of wind damage was lower in more heterogeneous forest landscapes. Edge effects might be a cause of higher risks for windthrows in the case of heterogeneous forest landscape (*e.g.*, Ruel, 2000).

The findings regarding snow breakage events were partly in contrast to those of windthrows. A larger volume of small-diameter trees (< 30 cm in dbh) increased the likelihood of snow breakage occurrence; this suggests that snow breakage would be more frequent in pole stands than in older mature stands or young growth stands (Y_GR). By contrast, younger stands with a larger volume of small-diameter trees (VOL_A) were more resistant to insect attacks. Our results also showed that severity of snow breakage decreased with a higher volume of medium-diameter trees (VOL_B), corresponding to early mature stands. Similar findings were reported by Jalkanen and Mattila (2000).

Not all relevant variables that influence natural disturbances were included in the multivariate analyses. Tree species composition may have a significant influence on disturbance frequency and on the amount of damaged trees. Several studies have reported that both are evidently higher in Norway-spruce–dominated forests (Nykänen *et al.*, 1997; Dobbertin, 2005). In our study the proportions of broadleaves (P_BR) and of Norway spruce (P_SP) were not included in the multivariate analyses because of high correlations to site variables. Additionally, the study area was not completely appropriate for testing the influence of tree species composition on natural disturbances due to the small number of compartments with a large portion of broadleaves. Among site variables, soil type (Kramer *et al.*, 2001) and soil pH (Mayer *et al.*, 2005) may have an important influence on natural disturbances. However, the data on soil characteristics in our data set were not of sufficient quality to be included in the analyses.

Another drawback of our data set was that salvage-cut trees were registered only according to the main disturbance agent leading to the damage or death of the tree. Some of these trees may have been previously damaged by another disturbance agent (wind or snow), making them more susceptible to other disturbances. For example, due to strong interactions between insect attacks and previous disturbances (Wermelinger, Duelli & Obrist, 2002), we can assume that some of the salvage-cut trees damaged by insect attacks were previously damaged by wind or snow. It is also possible that some of the cut trees damaged by wind or snow were previously attacked by insects or fungi. Additionally, salvage-cut trees were registered in the year when they were cut, which may have sometimes differed from the year when the disturbance occurred. In these cases, the residence time of dead wood on the forest floor was longer, which may have caused an increase in the severity of insect attacks compared to cases when trees were salvage-cut immediately. Thus, the timing of forest management measures could have an important influence on the number of trees killed by insects.

Forest management and resistance to natural disturbances

Forest management can be a very important factor in reducing the risk (Gardiner & Quine, 2000; Schelhaas, Nabuurs & Schuck, 2003) and severity of natural disturbances.

Nature-based forest management has the potential to mimic patterns of natural disturbances within forest management (Diaci, 2006). Our results show that some stand characteristics have an important influence on the occurrence and severity of natural disturbances. Despite the loose fit of the models (Tables II and III) due to the very stochastic nature of natural disturbances (Ruel, 2000; Kramer *et al.*, 2001; Schütz *et al.*, 2006) we believe the findings are useful for improving forest management.

The resistance of forest stands is known to be higher in uneven-aged, multi-layered stands than in even-aged, 1-layered stands (Mason, 2002; Bachmann & Dvorak, 2005). In accordance with our expectations, our study showed that a higher proportion of uneven-aged forests lowered the risk of windthrow occurrence and the risk and severity of snow disturbance occurrence. Although disturbances were lower in severity in compartments with a more heterogeneous forest landscape, those areas were more susceptible to the occurrence of windthrow and insect attack. Obviously, forest management that applies a specific silvicultural system can influence both the susceptibility of forests to natural disturbances and disturbance severity. To reduce the severity of disturbances our suggestion for the broader Alpine region is the application of small-scale irregular shelterwood, group, or single-tree selection systems (Schütz, 2005; Gartner *et al.*, 2007), which would result in a fine grained heterogeneous forest landscape.

Regular cutting (*i.e.*, thinning) could have both positive and negative impacts on stand resistance to natural disturbances depending on the type of thinning, site conditions, and the natural disturbance regime (Gardiner & Quine, 2000). In our case, previous regular cutting increased the risk of disturbance occurrence, a result that, in the case of snow disturbance, has also been reported by Nykänen *et al.* (1997), but the influence of cutting on the amount of damaged timber was significant only in the snow breakage model. The resistance of forest stands could be improved by using selective thinning from above, which should be carried out early in stand development and repeated frequently (Schütz *et al.*, 2006; Bodin & Wiman, 2007).

The tree species composition of the observed forest area has been dramatically changed over the past few centuries. Many researchers have reported that Norway-spruce–dominated stands are more prone to all 3 types of natural disturbances (Spiecker, 2000; Ulanova, 2000; Dobbertin, 2005). Increasing the amount of silver fir and European beech will therefore increase the resistance of forest stands to natural disturbances, which is the challenge to forestry and foresters in the region.

Acknowledgements

The study was supported by the Ministry of Science and Technology of the Republic of Slovenia (projects V4-0519 and L4-9231). The authors wish to thank Franci Cergol for the help on database creation and Tom Nagel. The comments of anonymous reviewers significantly improved the earlier version of the manuscript.

Literature cited

Allison, P. D., 1999. Logistic Regression Using the SAS System: Theory and Application. SAS Institute Inc., Cary, North Carolina.

Attiwill, P. M., 1994. The disturbance of forest ecosystems: The ecological basis for conservative management. Forest Ecology and Management, 63: 247–300.

Bachmann, P. & L. Dvorak, 2005. Sturmschäden in Abhängigkeit vom Bestandesaufbau in einem Plenterwaldgebiet. Pages 51–59 *in* M. Indermühle, P. Raetz & R. Volz (eds.), 2005. LOTHAR Ursächliche Zussammenhänge und Risikoentwicklung. Synthese des Teilprogramms 6. Umwelt-Materialen Nr.184. Bundesamt für Umwelt, Wald und Landschaft, Bern.

Bodin, P. & B. L. B. Wiman, 2007. The usefulness of stability concepts in forest management when coping with increasing climate uncertainties. Forest Ecology and Management, 242: 541–552.

Boncina, A., D. Robic & V. Mikulic, 2001. Standort, Struktur und Funktion slowenischer Wälder im Höhengradienten. Schweizerische Zeitschrift für Forstwesen, 152: 43–51.

Brang, P., 2005. Standortseinflüsse: Bodenversauerung, Wurzelsystem und Sturmschaden. Pages 69–77 *in* M. Indermühle, P. Raetz & R. Volz (eds.), 2005. LOTHAR Ursächliche Zussammenhänge und Risikoentwicklung. Synthese des Teilprogramms 6. Umwelt-Materialen Nr.184. Bundesamt für Umwelt, Wald und Landschaft, Bern.

Brang, P., W. Schönenberger, E. Ott & R. H. Gardner, 2001. Forests as protection from natural hazards. Pages 53–81 *in* J. Evans (ed.). The Forests Handbook. Blackwell Science Ltd., Oxford.

Brassel, P. & U.-B. Brändli, 1999. Schweizerische Landesforstinventar. Ergebnisse der Zweitaufnahme 1993–1995. Verlag Paul Haupt, Birmensdorf, WSL, BUWAL, Bern.

Canham, C. D., M. J. Papaik & E. F. Latty, 2001. Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. Canadian Journal of Forest Research, 31: 1–10.

Diaci, J., 2006. Gojenje gozdov: pragozdovi, sestoji, zvrsti, nacrtovanje, izbrana poglavja. University of Ljubljana, Ljubljana.

Dobbertin, M., 2002. Influence of stand structure and site factors on wind damage: Comparing the storms “Vivian” and “Lothar”. Forest Snow and Landscape, 77: 187–205.

Dobbertin, M., 2005. Erfassung der Bestandesdaten und Schäden auf dem repräsentativen 4×4-km Sanasilva-Netz. Pages 39–50 *in* M. Indermühle, P. Raetz & R. Volz (eds.), 2005. LOTHAR Ursächliche Zussammenhänge und Risikoentwicklung. Synthese des Teilprogramms 6. Umwelt-Materialen Nr.184. Bundesamt für Umwelt, Wald und Landschaft, Bern.

EEA, 2006. European Forest Types: Categories and Types for Sustainable Forest Management Reporting and Policy. EEA Technical Report, No.9/2006. European Environment Agency, Copenhagen.

FMP Bled, 2003. Forest Management Plan GGO Bled 2001–2010. Slovenia Forest Service, Ljubljana.

Franklin, J. F., 1993. The fundamentals of ecosystem management with applications in the Pacific Northwest. Pages 127–144 *in* G. H. Applet, N. Johnson, J. T. Olson & V. A. Sample (eds.). Defining Sustainable Forestry. Island Press, Washington, DC.

Frelich, L. E., 2002. Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen–Deciduous Forests. Cambridge University Press, Cambridge.

Gardiner, B. A. & C. P. Quine, 2000. Management of forests to reduce the risk of abiotic damage: A review with particular reference to the effects of strong winds. Forest Ecology and Management, 135: 261–277.

Gartner, A., V. Papler-Lampe, A. Poljanec & A. Boncina, 2007. Upostevanje katastrof pri nactrovanju in gospodarjenju z gozdovi na primeru vetroloma na Jelovici. Pages 153–176 *in* M. Jurc (ed.). Climate Changes: Impact on Forest and Forestry. University of Ljubljana, Ljubljana.

Gregorcic, G., B. Gregorcic & R. Bertalanic, 2002. Nevarni viharni vetrovi z juga. Znanost, 16-12-2002: 8–9.

Guisian, A. & N. E. Zimmermann, 2000. Predictive habitat distribution models in ecology. Ecological Modelling, 135: 147–186.

Hanewinkel, M., W. Zhou & C. Schill, 2004. A neural network approach to identify forest stands susceptible to wind damage. Forest Ecology and Management, 196: 227–243.

Hanewinkel, M., J. Breidenbach, T. Neeff & E. Kublin, 2008. Seventy-seven years of natural disturbances in a mountain forest area: The influence of storm, snow, and insect damage analysed with a long-term time series. Canadian Journal of Forest Research, 38: 2249–2261.

Hosmer, D. W. & S. Lemeshow, 2000. Applied Logistic Regression. 2nd Edition. John Wiley & Sons, New York, New York.

Jalkanen, A. & U. Matilla, 2000. Logistic regression models for wind and snow damage in northern Finland based on the National Forest Inventory data. Forest Ecology and Management, 135: 315–330.

Johann, E., 2006. Historical development of nature based forestry in Central Europe. Pages 1–17 *in* J. Diaci (ed.). Nature Based Forestry in Central Europe: Alternatives to Industrial Forestry and Strict Preservation. University of Ljubljana, Ljubljana.

König, A., 1995. Sturmgefährdung von Besänden im Alterklassenwald. Sauerländer, Frankfurt/Main.

Kramer, M. G., A. J. Hansen, M. L. Taper & E. J. Kissinger, 2001. Abiotic controls on long-term windthrow disturbance and temperate rain forest dynamics in southeast Alaska. Ecology, 82: 2749–2768.

Kräuchi, N., P. Brang & W. Schönenberger, 2000. Forests of mountainous regions: Gaps in knowledge and research needs. Forest Ecology and Management, 132: 73–82.

Lorimer, C. G. & A. S. White, 2003. Scale and frequency of natural disturbances in the northeastern US: Implications of early successional forest habitats and regional age distributions. Forest Ecology and Management, 185: 41–64.

Mason, W. L., 2002. Are irregular stands more windfirm? Forestry, 75: 347–355.

Mayer, P., P. Brang, M. Dobbertin, D. Hallenbarter, J.-P. Renaud, L. Walthert & S. Zimmermann, 2005. Forest storm damage is more frequent on acidic soils. Annals of Forest Science, 62: 303–311.

Nagel, T. A. & J. Diaci, 2006. Intermediate wind disturbance in an old-growth beech–fir forest in southeastern Slovenia. Canadian Journal of Forest Research, 36: 629–638.

Nilsson, C., I. Stjernquist, L. Bärring, P. Schylter, A. M. Jönsson & H. Samuelsson, 2004. Recorded storm damage in Swedish forests 1901–2000. Forest Ecology and Management, 199: 165–173.

Nykänen, M.-L., H. Peltola, C. P. Quine, S. Kellomäki & M. Broadgate, 1997. Factors affecting snow damage of trees with particular reference to European conditions. Silva Fennica, 31: 193–213.

Oberdorfer, E., 2001. Pflanzensoziologische Exkursionsflora für Deutschland und angrenzende Gebiete: 8. Auflage. Eugen Ulmer GmbH & Co., Stuttgart, Germany.

Ogris, N., S. Dzerovski & M. Jurc, 2004. Windthrow factors: A case study on Pokljuka. Zbornik gozdarstva in lesarstva, 74: 59–76.

Pfeffer, A., 1995. Zentral- und westpalaearktische Borken- und Kernkaefer (Coleoptera: Scolytidae, Platypodidae). Pro Entomologia, Basel, Swiss.

Pickett, S. T. A. & P. S. White, 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, London.

Pielou, E. C., 1975. Ecological Diversity. John Wiley & Sons, New York, New York.

Ruel, J.-C., 2000. Factors influencing windthrow in balsam fir forests: From landscape studies to individual tree studies. Forest Ecology and Management, 135: 169–178.

Schelhaas, M.-J., G.-J. Nabuurs & A. Schuck, 2003. Natural disturbances in the European forests in the 19th and 20th centuries. Global Change Biology, 9: 1620–1633.

Schütz, J.-P., 2005. Einfluss verschiedener Faktoren auf Art und Ausmass der Sturmschäden: Windcharacteristic und Sturmschäden im Raum Reusstal-Limattal. Pages 29–38 *in* M. Indermühle, P. Raetz & R. Volz (eds.). LOTHAR Ursächliche Zussammenhänge und Risikoentwicklung. Synthese des Teilprogramms 6. Umwelt-Materialen Nr.184. Bundesamt für Umwelt, Wald und Landschaft, Bern.

Schütz, J.-P., M. Götz, W. Schmid & D. Mandallaz, 2006. Vulnerability of spruce (*Picea abies*) and beech (*Fagus sylvatica*) forest stands to storms and consequences for silviculture. European Journal of Forest Research, 125: 291–302.

Seymour, R. S., A. S. White & P. G. deMaynadier, 2002. Natural disturbance regimes in northeastern North America: Evaluating silvicultural systems using natural scales and frequencies. Forest Ecology and Management, 155: 357–367.

Slovenia Forest Service (SFS), 2007. TIMBER: The Database of Cutting for the Period 1979–2006. Slovenia Forest Service, Ljubljana.

Spiecker, H., 2000. Growth of Norway spruce (*Picea abies* [L.] Karst.) under changing environmental conditions in Europe. Pages 11–26 *in* E. Klimo, H. Hager & J. Kulhavý (eds.). Spruce Monocultures in Central Europe: Problems and Prospects. EFI Proceedings No.33, Joensuu.

Splechtna, B. E. & G. Gratzer, 2005. Natural disturbances in Central European forests: Approaches and preliminary results from Rothwald, Austria. Forest Snow and Landscape Research, 79 (1/2): 57–67.

Stathers, R. J., T. P. Rollerson & S. J. Mitchell, 1994. Windthrow Handbook for British Columbia Forests. Working Paper 9401. BC Ministry of Forests, Victoria, British Columbia.

Ulanova, N., 2000. The effects on windthrow on forests at different spatial scales: A review. Forest Ecology and Management, 135: 155–167.

Valinger, E. & J. Fridman, 1997. Modelling probability of snow and wind damage in Scots pine stands using tree characteristics. Forest Ecology and Management, 97: 215–222.

Wermelinger, B., P. Duelli & M. K. Obrist, 2002. Dynamics of saproxylic beetles (Coleoptera) in windthrow areas in alpine spruce forests. Forest Snow and Landscape Research, 77: 133–148.

Woods, K. D., 2004. Intermediate disturbance in a late-successional hemlock–northern hardwood forest. Journal of Ecology, 92: 464–476.

Worrall, J. J., T. D. Lee & T. C. Harrington, 2005. Forest dynamics and agents that initiate and expand canopy gaps in *Picea – Abies* forests in Crawford Notch, New Hampshire, USA. Journal of Ecology, 93: 178–190.

Zeibig, A., J. Diaci & S. Wagner, 2005. Gap disturbance patterns of a *Fagus sylvatica* virgin forest remnant in the mountain vegetation belt of Slovenia. Forest Snow and Landscape Research, 79: 69–80.

3 DISCUSSION WITH CONCLUSIONS

3.1 THE USE OF ARCHIVAL DATA IN THE LONG-TERM FOREST STAND DYNAMICS RESEARCH

Archival forest inventory data, gathered mainly in forest management plans, enable detailed reconstruction of long-term stand dynamics and make possible the evaluation of its main influential factors as well as their detailed investigation. Methods based on archival data sources enable stand dynamics research in a substantially shorter time period compared with palynology or dendrochronology (Agnoletti and Anderson, 2000). However, such data sources may provide temporarily and spatially high resolution data on forest stand parameters (Axelsson et al., 2002). But nevertheless, archival data describe only the state of forest stands at a certain point in time, which is just one of many, though maybe only slightly different, states over the long time period of forest stand history. This fact needs to be greatly considered when intepreting the results. Moreover, considerable caution is always needed when interpreting the results and drawing conclussions when dealing with historical data sources (Swetnam et al., 1999).

We encountered some problems during the acquisition of the data and the preparation of the database; some forest management maps were missing, different methodologies of forest inventories were used, dbh distributions of forest stands were provided in variously broad (2-, 5-, or 10-cm) dbh classes, different measuring thresholds were used, tree species composition was provided by groups of tree species, and data on some forest stand parameters in some inventories were incomplete. The majority of problems were solved effectively, but some minor imperfections were still built into the GIS database. Nevertheless, when investigating long-term forest stand dynamics, we were more concerned with the relative dynamics of forest stand parameters than with the absolute values. However, when investigating natural disturbance occurrence and severity and their influential factors, a much shorter time span was considered for which reliable data on stand characteristics, site conditions, and forest management measures (i.e. salvage and regular cutting) were available at very detailed spatial (i.e. compartment) and temporal (i.e. annual) scales. Therefore, we believe our databases were relevant for examining the research objectives, especially considering that they span a relatively long period and are of relatively detailed spatial resolution.

Our study confirmed that archival data from old forest management plans make it possible to study forest stand dynamics at different spatial levels, from larger forest regions to (sub)compartments. Although results were mainly shown for larger forest areas in our study, it is also possible to study long-term dynamics at the (sub)compartment spatial level based on how the database was constructed. In confirmation, some analyses were made at the stand spatial level, i.e. changes in growing stock, tree size diversity, and recruitment rate. However, a more detailed analysis of other stand parameters at a (sub)compartment spatial level using our database might be unreasonable and too rough. For such an analysis the database should be supplemented with the data at the stand level within the compartment, which would be possible using the high-resolution forest stand maps for recent decades; before the 1950s the compartment borders usually coincided with the forest stand borders. Additionally, the use of (sub)compartments as a spatial basis for the GIS database may be debatable since their area and shape are unequal. Its use might be appropriate in the analysis of the long-term stand dynamics, but much less so in the modelling procedures, where basic study areas are better if they are of equal size and shape (i.e. square area or pixel) (Jørgensen and Bendoricchio, 2001). However, in our study, as well as in some others (Hanewinkel, 2005; Scrinzi et al., 2007; Hanewinkel et al., 2008), this impediment was solved by using appropriate statistical methods.

3.2 THE DYNAMICS OF SILVER FIR-EUROPEAN BEECH FORESTS OVER THE LAST CENTURY

The structure and composition of the investigated silver fir-European beech forests have seen noticeable changes in dynamics over the last century. Changes in the diameter distribution of trees, stand volume, tree species composition, and other analysed stand parameters have been considerable over the century-long time period. Some important differences, but also some similarities, were observed in the stand dynamics between the study areas.

The observed dynamics of diameter distribution of trees in the analysed forest stands suggested two different courses of forest stand development: “a regeneration” of stands in Trnovo and Jelovica, and “an ageing” of stands in Leskova dolina. In the first two cases, an increase in the total number of trees (i.e. stand density) and in quantity of small-diameter trees (dbh=10-29 cm) was observed, indicating “the regeneration” of those stands in the long-term. In contrast, in Leskova dolina an increase in the quantity of large-diameter trees (dbh≥50 cm) was found in combination with the reduction in the total number of trees. These findings are far more worrying than those from Trnovo or Jelovica since they have been mainly caused by insufficient regeneration and recruitment of saplings into the tree layer and consequently delayed regeneration cuts in those stands. This impediment has not been completely tackled yet since fir and sycamore recruitment is still relatively poor there, which could not be stated for beech or spruce. Spruce recruited mainly in the artificially established forest stands, but less in the naturally regenerated stands.

Tree species composition was also subjected to substantial changes during the last century. In addition, there were significant differences between study areas. Typical characteristics of the investigated fir-beech stands were a reduction in fir proportion and increases in the proportions of spruce or broadleaves in the last four decades. In our opinion, these findings correspond more to fluctuations in dominance among the main tree species in fir-beech forests (Šercelj, 1996; Wick and Möhl, 2006; Vrska et al., 2009; Diaci et al., 2010a) than to the “natural process” of their alternation (Korpel, 1995). Observed fluctuations were more a consequence of anthropogenic than natural influential factors, foremost of which was past forest management. The dynamics of tree species composition differed between fir-beech forests in the Dinaric Mountains, where major fluctuations between fir and beech occurred (albeit in different time frames), and fir-beech forests in the Alps, where spruce was the dominant tree species throughout the entire observation period. However, more close-to-nature oriented forest management in the last five decades in the Alps triggered the promotion of broadleaves and fir, which has not been evidenced yet in the proportions of tree species in the stand volume, but already has been noted in the tree species composition of the regeneration (Slovenia Forest Service, unpublished; Jerina et al., unpublished).

The main common characteristic of the observed fir-beech forest stands was an increase in the average stand volume. It was mainly a consequence of the deliberate accumulation of stand volume increment and a rise of the target stand volume above 400 m^3 ha^{-1} due to overexploitation in the 19th century and heavy recovery cuttings after World War II (FMP Leskova dolina, 1954; Gašperšič, 1967; Kordiš, 1993). But, some varying environmental conditions and low-intensity forest management in the last few decades have also had some effects.

Fir, as one of the main tree species of the fir-beech forest type and an important species of Central European mountain forests in general (Schütt, 1999; Senn and Suter, 2003; EEA, 2006), underwent the most large-scale changes compared with beech and spruce, the other main tree species. Our analysis of fir diameter structure, which also indicated its age structure, revealed two countervailing dynamics. Currently, the fir population in the Alps is younger than it was at the beginning of the observation period. On the contrary, the fir population in the Dinaric Mountains was noticeably younger a century ago than it is today. Moreover, the fir population in the Alps is much younger than the population in the Dinaric Mountains when considering its relative abundance in the total number of trees; however, its absolute presence (number of trees, stand volume) is much higher in the latter area.

In the Dinaric Mountains, the main tree species, fir and beech, were found to alternate in their dominance. Reciprocal replacement of fir and beech, in the sense that fir regenerates with higher probability under mature beech trees and vice versa, is expected to occur due to allelopathic relationships between both species (Gašperšič, 1974; Oliver and Larsen, 1996; Diaci et al., 2010b) or due to the prevalent disturbance regime and differences in shade-tolerance between fir and beech seedlings, saplings, and pole-stage trees (Nagel et al., 2010). Additionally, current environmental conditions obviously promote beech over fir, while fir abundantly regenerated at one time in the past (Gašperšič, 1967; Bončina et al., 2003; our study) and is currently in regression (Diaci et al., 2010a, 2010b; Ficko et al., 2011). Our study and several others (Heuze et al., 2005; Ficko and Bončina, 2006; Hockenjos, 2008; Anić et al., 2009; Bončina et al., 2009; Diaci et al., 2010b; Ficko et al., 2011) declared a continued decline in its share in the near future, probably to the level before the first intensive forest exploitation started. However, this trend is not the case everywhere. Some observations showed that on certain sites fir regenerates and recruits well in Slovenia (e.g. Bončina et al., 2009; Simončič and Bončina, 2009) and elsewhere (e.g. Čavlović et al., 2006; Dobrowolska and Veblen, 2008). However, as in forests on the Bohor Mountain (Simončič and Bončina, 2010) and some other mainly acidic sites in Slovenia, currently fir abundantly regenerates and recruits into the canopy (Bončina et al., 2009). Obviously fir is in progression there, and in the future, regression of beech, which is now in the mature stage, could be expected. It is highly likely that fir needs "a window of opportunity", a co-occurrence of appropriate environmental conditions, such as low enough densities of large ungulates, full- and partial-seed years, an accordant disturbance regime, and appropriate mature stand structure and composition, for its abundant regeneration and successful recruitment into the stand canopy (Frelich and Lorimer, 1985; Linder, 1998; Senn and Suter, 2003).

3.3 FACTORS INFLUENCING LONG-TERM FOREST STAND DYNAMICS IN SILVER FIR-EUROPEAN BEECH FORESTS

The observed dynamics of fir-beech forest stands is underpinned by the complexity of natural and anthropogenic factors; however, it is the latter that stands out. Differences in past forest use, regimes of abiotic and biotic natural disturbances, and site conditions seem to be the most important impact factors in the long-term dynamics of fir-beech forest stands in Slovenia.

Past forest use, mainly charcoal and potash production for the iron and glass industry, as well as cattle grazing, slash-and-burn, resin production, and small, uncontrolled cutting had considerably altered forest stand structure and composition even before the first forest inventory was done and regular forest management started (Veber, 1986; Kordiš, 1993; Perko, 2002; Papež and Černigoj, 2007). Study areas differ in past forest uses and their spatiotemporal impacts on the structure and composition of forest stands.

In Jelovica forest stands were devastated at the beginning of the observation period because of overexploitation in the 18th and 19th centuries, when mainly beech timber was used for charcoal and potash production utilised in the iron and glass industry (Veber, 1986). Spruce was planted and already favoured over broadleaves at that time. In addition, cattle grazing was quite intensive even before that period and has been maintained in a more extensive nature until today (Smolej, 1984; FMP Jelovica, 2002).

In Trnovo forest stands were already regularly managed in the 18th century; a mainly regular shelterwood silvicultural system was practiced. Before that, charcoal and resin production, cattle grazing, and small-scale, uncontrolled cutting were present in these forests, which, at that time, were mainly beech forests with some fir and spruce (Papež and Černigoj, 2007).

Forest stands in Leskova dolina had not been intensively exploited until the 18th century. Before that time only extensive forest use, such as cattle grazing, slash-and-burn, and hunting, were present (Kordiš, 1993). Even though the stocking of forests in the study areas was generally low at the period in which our study starts, the baseline states of the analysed fir-beech forest stands differed noticeably between the study areas, substantially affecting the dynamics of the investigated forest stands.

During the studied period of regular forest management, the forest management concept was the most important factor influencing the long-term stand dynamics. Observed deviations in stand dynamics between study areas occurred mainly due to differences in the applied silvicultural systems, but also to differences in the regime and to the importance of different natural disturbances in a particular study area. The impact of past forest management and natural disturbances on the long-term forest stand dynamics will be discussed and provided by individual study areas.

Jelovica study area

In Jelovica the observed long-term stand dynamics are a reflection of the typical forest management in the Alpine region several decades ago, practices which included mainly large-scale cutting, the planting of spruce, and the weeding out of broadleaves (Smolej, 1984; Veber, 1986; Johann, 2007). Such a forest management concept was practiced until the mid-20th century, leading to the current domination of spruce and more even-aged forest stands than uneven-aged stands. However, in limited locations "plentering" was already practiced at the end of the 19th century (FMP Jelovica, 1899; Veber, 1986). In the 1960s close-to-nature oriented forest management, in which a small-scale irregular shelterwood system has been mainly practiced, was applied in these forests. It has resulted in a shift towards fine-grained horizontal structure of the forest landscape (Klopčič and Bončina, 2010) and in a small increase in the proportion of broadleaves in the stand volume over the last two decades, but more evidently in better regeneration and recruitment of fir and broadleaves in these forest stands (Slovenia Forest Service, unpublished; Jerina et al., unpublished; our study). It is expected that there will be a greater increase in their proportion of stand volume in the next few decades, when saplings of fir and broadleaves recruit into the tree layer and canopy.

Besides forest management, natural disturbances have had a noticeable influence on forest stand dynamics in these forests. In the last three decades, salvage cutting due to natural disturbances, mainly wind, snow, and insect damage, represented more than half of the total annual cut. This result indicates the relevant role of natural disturbances in the forest stand dynamics of these forests, which represent a serious impediment to forest management. We assume that a similar conclusion could be made for the broader alpine region where the natural tree species composition of forest stands has been substantially altered. However, even if very little could be done to prevent the occurrence of catastrophic high-severity natural disturbances, several measures could be carried out to improve the resistance and resilience of forest stands to intermediate and low-severity, small-scale disturbances.

We found that several site, stand, and past forest management variables significantly influenced both the occurrence and severity of natural disturbances. However, only stand characteristics and silvicultural measures are variables that can be influenced by forestry experts. Both the univariate and multivariate analyses showed that the stand resistance to windthrow was found to be higher in pole stage stands with a high portion of small-diameter trees (dbh=10-29 cm) and in uneven-aged stands, while a higher share of mature stands with a high portion of large-diameter trees (dbh≥50 cm), a high proportion of spruce (significant only in univariate analysis; hereafter UNI), and a high share of regeneration stands in a compartment increased the probability of windthrow occurrence. The latter could be related to the edge effect, which increases the susceptibility of stands to windthrow occurrence (e.g. Ruel, 2000; Pellikka and Järvenpää, 2003; Ogris et al., 2004; Schütz, 2005; Schütz et al., 2006). The probability of snow breakage occurrence was decreased by a higher share of uneven-aged stands in a compartment and a higher proportion of broadleaves in the stand volume (UNI), while it was enhanced by a higher share of pole stage stands in a compartment, a higher proportion of small-diameter trees, and a higher proportion of spruce in the stand volume (UNI). In addition, insect outbreaks may be hindered by a higher proportion of small-diameter trees and a higher share of uneven-aged stands (UNI), while the probability of their occurrence was increased by a higher proportion of large-diameter trees, a higher proportion of spruce (UNI), and a more heterogeneous forest landscape with higher shares of regeneration and stands in the rejuvenation stage, which could point to the relationship between the internal forest edge and the occurrence of insect attacks (Peltonen, 1999; Gilbert et al., 2005). In general, the resistance of forest stands could be enhanced by promoting uneven-aged structure in forest stands with an admixture of 20-40 % of broadleaves in the stand volume.

The resistance of forest stands can be substantially influenced by silvicultural measures, such as tending and thinning. The first measure is particularly important in regulating and directing tree species composition, while the second is more important in improving the mechanical stability of forest stands. The latter should be carried out as selective thinning from above, which should be carried out early enough in the stand development and repeated frequently (Schütz et al., 2006; Bodin and Wiman, 2007).

Large ungulates were a minor disturbance in the past in these forests. A more important disturbance was cattle grazing, especially in the period between the 17th and the 19th century (Smolej, 1984; Veber, 1986). However, large ungulate densities have risen in recent decades, resulting in increased browsing pressure on the regeneration. In 2004-2008 average calculated densities based on annual game harvesting data were 1.8 red deer km^{-2}, 0.6 roe deer km^{-2}, 0.5 chamois km^{-2}, and 0.05 mouflon (*Ovis musimon* Pallas) km^{-2} (Jerina, 2008; Stergar et al., 2009).

Trnovo study area

In Trnovo, the observed long-term stand dynamics is mainly a result of the regular shelterwood silvicultural system practiced from the late 18th century until the 1960s, when mainly an irregular shelterwood system was applied (Kordiš, 1993). The increase in fir proportion in the first half of the 20th century was a consequence of abundant fir regeneration in the second half of the 19th century and its subsequent intense promotion by weeding out beech and providing more growing space for fir regeneration (FMP Trnovo, 1887). Similar stand and fir population dynamics was observed in the Leskova dolina study area. In the last five decades, the irregular shelterwood system, practiced in intermediate to larger cutting areas, promoted beech, spruce, and other broadleaves at the expense of fir. Fir recruitment rate was the lowest among the study areas, and the future of fir in these forests is very questionable and highly unpredictable.

Besides forest management practices, large ungulates also might have played a role in the recruitment rate of fir. The average calculated data on large ungulate densities in the period 2004-2008 were 0.3 red deer km^{-2}, 3.7 roe deer km^{-2}, 2.1 chamois km^{-2}, and 0.06 mouflon km^{-2} (Jerina, 2008; Stergar et al., 2009). According to these data the browsing pressure was lower in Trnovo compared with some other parts of the Dinaric Mountains (i.e. Leskova dolina), since the density of the red deer, which is the greatest consumer of green biomass among these species, was much lower in Trnovo than in Leskova dolina. Though, other large ungulate species, i.e roe deer and chamois, may have significant impacts on the regeneration and recruitment of tree species and fir in particular. In addition, according to Papež and Černigoj (2007) and forest management plans (e.g. FMP Trnovo, 2003), natural disturbances, especially windthrow, but also snow breakage, might play an important role in the long-term stand dynamics in forests on the Trnovski gozd plateau. However, long-term data on natural disturbance occurrences or annual salvage cut have not yet been gathered, representing a possibility for a future analysis and for an update of our study.

Leskova dolina study area

Forest stands in Leskova dolina were managed according to the principles of the“plenter” silvicultural system from the beginning of the 20th century (Schollmayer, 1906) until the 1960s. Conifers were strongly preferred over broadleaves in this time period, which led to the domination of fir in the stand volume, even over 90 % in some compartments. This was possible due to the very abundant fir regeneration in the first half of the 19th century when the majority of the current mature fir trees germinated. In the 1960s, a small-scale irregular shelterwood silvicultural system was applied, and a combination of both systems has been in use ever since (Kordiš, 1993). Despite applying a silvicultural system favourable to shade-tolerant species (i.e. fir and beech) regeneration, insufficient recruitment of fir, mainly due to high browsing pressure and increased stocking of forest stands, led to noticeable changes in the structure and composition of these stands.

Large ungulate browsing is the main natural disturbance influencing the long-term stand dynamics in these forest stands. The reported densities in 2004-2008 were 3 red deer km^{-2}, 1.3 roe deer km^{-2}, and 0.04 chamois km^{-2} (Jerina, 2008; Stergar et al., 2009). Their influence is reflected in hindering the natural regeneration and recruitment of sapling into the tree layer, especially more palatable tree species like fir and sycamore. The reduction in recruitment of small-diameter fir to the stand canopy was found to be caused not only by high browsing pressure, but also by some additional factors, such as the structure (i.e. stand density) and composition of forest stands as well as the intra- and inter-specific relationships in the forest ecosystem. Abiotic and other biotic natural disturbances play only a minor role in these forests (FMP Leskova dolina, 2004). This might be because of their pronounced uneven-aged structure, which was frequently reported to be more resistant to natural disturbances (e.g. Dvorak et al., 2001; Dobbertin, 2002; Bachmann and Dvorak, 2005) and was also confirmed in a part of our study.

Site conditions are an important component influencing "natural" forest stand structure and composition and may vary within the same forest type due to differences in microsite and mesosite conditions (Oliver and Larsen, 1996; van der Maarel, 2005). They also have a significant impact on the occurrence and severity of some abiotic and biotic natural disturbances (e.g. Nykänen et al., 1997; Kramer et al., 2001; Wermelinger, 2004; Dobbertin, 2005; Evans et al., 2007; Seidl et al., 2007; Hanewinkel et al., 2008), but less so on the impact of large ungulates. However, the latter is somewhat connected to microsite conditions, since fir is relatively more abundant on rocky and steep sites, where the transitiveness for large ungulates is lower than in the majority of forests (Jerina, 2008; Jerina, unpublished; personal observations). In addition, vertically heterogeneous stands made by "plentering" are established on such sites in order to maximize the protection function of the stand and to promote fir regeneration and recruitment (Klopčič and Bončina, unpublished).

Additionally, factors other than those discussed may also noticeably impact the dynamics of mixed fir-beech forest stands, e.g. inter- and intraspecific relationships like autoinhibition or allelopathy (Oliver and Larsen, 1996: p. 181), differences in competitiveness and natural resource usage between tree species (van der Maarel, 2005: p. 208), the impact of climate change (Lindner et al., 2010), fir decline due to different reasons (Larsen, 1986; Elling et al., 2009; Ficko et al., 2011), or the introduction and spread of non-native tree species (Schuster et al., 2008).

3.4 IMPLICATIONS FOR FOREST MANAGEMENT AND SUGGESTIONS FOR FUTURE RESEARCH

The forest management regime, and the applied silvicultural system in particular, was found to have a significant impact on changes in forest stands, as was expected. Therefore, the choice and application of the silvicultural system in stands of a particular forest type needs to take into consideration not only "natural" forest stand dynamics, found in old-growth or near-natural forests of a particular forest type (e.g. Korpel, 1995; Bončina, 2000; Diaci, 2006; Nagel et al., 2007), but also site conditions, current and potential "natural" stand characteristics, and forest management objectives. In this context, in the fir-beech forest type we suggest the application of silvicultural systems that create small-scale canopy gaps and generate a vertically and horizontally heterogeneous forested landscape with stands of mainly uneven-aged structure. However, this recommendation should not be generalized and strictly followed. In "natural" long-term forest stand dynamics, intermediate and large-scale high-severity natural disturbances also take place (e.g. Splechtna and Gratzer, 2005; Nagel et al., 2007; Nagel and Svoboda, 2008; Firm et al., 2009). Disturbances of such severity could also be mimicked in forest management, but site conditions and stand characteristics have to be strongly considered. For example, in the fir-beech forest type, large-scale cutting could be practiced on sites where beech makes up a substantial proportion of the tree species composition, is expected to dominate in the future, and (advanced) regeneration is already present in a stand. In this case, the degradation and karstification of forest ground should not cause problems since beech usually regenerates abundantly and quickly after cutting and usually predominates in the regeneration even in larger canopy gaps (e.g. Nagel et al., 2006; Klopčič and Diaci, 2008).

Forest stand management can play a significant role in reducing the hazard and severity of natural disturbances (e.g. Gardiner and Quine, 2000). Forest stand structure and composition significanty influence the occurrence and severity of natural disturbances. Uneven-aged, multi-layered stand structures were often found to be more resistant to natural disturbances than even-aged, uniform stand structures (e.g. Nykänen et al., 1997; Dvorak et al., 2001; Dobbertin, 2002; Bachmann and Dvorak, 2005), and this was also confirmed in our study. However, some adverse results also were reported (e.g. Nykänen et al., 1997; Mason, 2002; Dobbertin, 2005). Additionally, pure conifer-dominated forest stands, especially pure spruce stands, were frequently reported to be more prone to natural disturbances than mixed stands (Nykänen et al., 1997; Jalkanen and Mattilla, 2000; Dobbertin, 2002, 2005; Wermelinger et al., 2002; Spiecker et al., 2004; Schütz, 2005; Schütz et al., 2006; Hanewinkel et al., 2008). The noticeable admixture of broadleaves (≥ 20 %) in forest stands significantly lowered their susceptibility to windthrow (Schütz et al., 2006; our study), snow damage (Nykänen et al. 1997; our study), and other disturbances such as insect and fungi outbreaks (Knoke et al., 2008). Thinning is an important silvicultural measure in reducing the risk and severity of natural disturbance occurrence in the long-term. Although it was found to increase the susceptibility of stands to natural disturbances in the short term, it was discussed that in the long-term, thinning improves the mechanical stability of trees and consequently of stands, but has to be intensive enough in terms of early commencement, frequent return, and thinning from above (e.g. Schütz et al., 2006).

Wildlife populations, particularly large ungulates, have a significant impact on the long-term and short-term stand and fir dynamics (Gil, 1992b; Motta, 1996; Senn and Suter, 2003; Heuze et al., 2005; Diaci et al., 2010b; our study). Our results on the regeneration analysis in fenced and non-fenced areas in Leskova dolina showed a substantial impact of large ungulates, particularly red deer, on fir and sycamore regeneration especially, which in the non-fenced areas did not grow more than 50 cm and 130 cm in height, respectively. However, large ungulates have obviously not been the only impediment for management and conservation of fir in fir-beech forests. In Trnovo red deer densities were the lowest among the study sites, while the recruitment rate of silver fir was also the lowest. In Leskova dolina a reduction in fir recruitment into the stand canopy had already been recorded during periods of low red deer densities. Additionally, on certain sites fir regenerates and recruits much better (e.g. Čavlović et al., 2006; Jerina, 2008; Bončina et al., 2009; Simončič and Bončina, 2009). Consequently, a question arises as to what densities of large ungulates would allow fir to still successfully regenerate and recruit into the stand canopy. A fact that strongly influences the search for the answer to this question is the delayed impact of browsing on the regeneration and the recruitment of trees, especially slow-growing tree species like fir. Considering this, the impact of current browsing will become apparent only after several decades or even a century. Moreover, there may not be a single answer to this question, which may depend on several factors, such as site conditions influencing the regeneration of fir, the transitiveness of a site and its attractiveness as a habitat for large ungulates, the food capacity of the area (e.g. the portion of grass grazing areas, the portion of regeneration and stands in the rejuvenation stage, the amount of herbs and shrubs within stands), large ungulate species present in the area, and human disturbance in the area (e.g. Jerina, 2008; Stergar et al., 2009; Jerina, unpublished). Therefore, the main intention of forest ecosystem management has to be a better understanding and sensible management of forest stand dynamics with all ecosystem components having equal priority in the process of forest planning and management. In fir-beech forests, one of the main objectives of forest management should be to effectively balance stand and large ungulate components of the forest ecosystem. Both fir and large ungulates have probably been an important component of this forest ecosystem for millennia. Therefore, we should find a convenient solution to maintain both large ungulates and fir.

In order to solve the abovementioned imbalance, additional research and continued detailed monitoring of trends in large ungulate densities and browsing pressure should be carried out.

In the investigation of the impact of large ungulates on long-term stand dynamics, more study areas with adequate long-term data on game densities and stand parameters would certainly provide additional knowledge and experience. Moreover, it would enable the comparison of long-term large ungulate impacts between study areas of different stand structure and composition and of various large ungulate densities and species composition.

Future research on long-term forest stand dynamics should expand to other forest types that would provide additional knowledge and experience to transfer into forest practice; however, adequate forest inventory data that are preserved and available in the form enabling the investigation of long-term stand dynamics are lacking in most forest regions. In addition, new methodological approaches could be applied. A conversion of the GIS data from vector to raster format with resoultion of e.g. 25 m × 25 m would enable detailed investigations of forest stand dynamics, as well as the usage of sophisticated modelling approaches (Jørgensen and Bendoricchio, 2001; Seidl et al., 2011).

Further, the study of natural disturbances and their impact on long-term stand dynamics, but also of their influential factors, could be improved by extending the study area on sites where both uneven-aged and even-aged forest stands have a wide range of proportions of broadleaves in the stand volume. Such a study would provide more relevant findings regarding the influence of forest stand structure and composition on the occurrence or severity of natural disturbance. Since natural disturbances play a noticeable role there (Papež and Černigoj, 2007), the Trnovo study area would be an appropriate research subject to carry out such a study.

The forest ecosystem is a complex and dynamic system. Forest stand structure and composition will never be stable because the forest ecosystem continuously responds to changes in its environment (Oliver and Larsen, 1996; Bernadzki et al., 1998; Frelich, 2002). However, "...nature has a functional, historical, and evolutionary limits. Nature has a range of ways to be, but there is a limit to those ways, and therefore, human changes must be within those limits" (Christensen et al., 1996). The primary objectives of the long-term forest stand dynamics research and historical ecology in general should be to define those limits in different forest types and to gain new knowledge on the patterns and processes within long-term forest stand dynamics of a particular forest type (Swetnam et al., 1999). Applying historical knowledge into forest management practice is a necessity, since (uneven-aged) forest management should be oriented towards managing the processes in the forest ecosystem and less towards maintaining static structures.

4 SUMMARY

4.1 SUMMARY

Within a particular range of variability, changes in the structure and composition of forest stands are a fundamental part of their long-term stand dynamics. The present structure and composition of forest stands are a complex interplay between site conditions, inter- and intra-specific relationships, and natural and anthropogenic disturbances. The latter have been the most important factor driving the dynamics of temperate forests in the last several centuries. However, natural disturbances may also play an important complementary role in long-term stand dynamics. A detailed knowledge of forest stand dynamics, as well as the processes and factors influencing this dynamics, is of great importance, especially when close-to-nature forest management is utilised.

When examining long-term forest stand dynamics, many different investigative methods and data sources are used. Archival forest inventory data were a long-neglected data source, but have recently gained much more attention since they may make it possible to quantify changes in forest structure and composition in the long-term and enable better understanding of impacts of a changing disturbance regime over the past several decades or centuries.

Few studies have investigated the long-term dynamics of silver fir-European beech forests, and even fewer have analysed the variability of the dynamics on the forest stand and landscape spatial level between geographically diverse study areas within the same forest type. Therefore, the objectives of our study were 1) to investigate the dynamics of the structure and composition of mainly uneven-aged fir-beech forests in spatially dislocated study areas over the last century using archival data, with an additional particular focus on silver fir, 2) to identify the main influential factors and to evaluate their role in driving long-term forest stand dynamics, and 3) to examine factors influencing the occurrence and severity of natural disturbances as one of the main influential factors of long-term stand dynamics in the alpine fir-beech forests.

To achieve these objectives, three spatially dislocated study areas within the fir-beech forest type were chosen in Slovenia, the Jelovica study area representing alpine fir-beech forests, the Trnovo study area representing fir-beech forests with characteristics of Dinaric, alpine, and Submediterranean vegetation, and the Leskova dolina study area representing Dinaric fir-beech forests. Archival forest stand data, gathered mainly in old forest management plans, and archival forest management maps were used to create the GIS database and to analyse the

long-term stand dynamics of mainly uneven-aged forest stands. The GIS database covered the time periods 1899-2002 for the Jelovica study area, 1897-2003 for the Trnovo study area, and 1912-2004 for the Leskova dolina study area. Changes in forest stands were evaluated with selected structural and compositional indicators: dbh structure, stand volume by using stand volume index SVI, tree size diversity by using the Gini coefficient GC, tree species composition, and recruitment rate in the last forest inventory period by using recruitment rate index RRI. In addition, explanatory information from the textual part of archival forest management plans and wild game and timber harvesting records were used to identify and investigate the main influential factors of long-term forest stand dynamics.

Over the century-long time period, all studied stand parameters showed noticeable dynamics. Considerable changes were demonstrated in the diameter distribution of trees, stand volume, tree species composition, and tree size diversity. However, significant differences, as well as some similarities, in forest stand dynamics were observed at a regional spatial scale inside the same fir-beech forest type.

The main common characteristic of the analysed forest stands was an increase in stand volume, which increased by 1.6, 1.6 and 2.4 times in Jelovica, Trnovo and Leskova dolina, respectively. Similarly, the dbh structure of forest stands changed noticeably in the analysed period, but in contrast to stand volume, changes differed between the study areas. Changes in dbh structure indicated two different directions of forest dynamics: an increase in stand densities and quantity of small-diameter trees ("regeneration of stands") in Jelovica and Trnovo, and an increase in quantity of large-diameter trees combined with the reduction in the number of trees ("ageing of stands") in Leskova dolina. Diverse dynamics between the study areas were also observed in tree size diversity within forest stands. In the observed period, the GC increased by 1.14 times in Leskova dolina, indicating a clear trend of forest stands towards becoming more diverse in their tree size diversity (more uneven-aged), but stagnated in Trnovo, suggesting only minor changes in tree size diversity, and decreased by 1.6 times in Jelovica, where stands changed from stands with the highest tree size diversity at the beginning of the observation period to stands with the lowest tree size diversity (more even-aged) at the end of the observation period. The tree species composition of the studied forests underwent profound changes in the observation period. In general, the proportion of broadleaves and spruce increased significantly, while a decrease in the proportion of fir was observed in recent decades. Significant differences in tree species proportions were found between study areas in all ten-year time periods. In Jelovica spruce was the dominant tree species throughout the study period, while in Trnovo and Leskova dolina, fluctuations of the dominant tree species, fir and beech, were recorded, albeit in different time frames. Also, the recruitment rate significantly differed between study areas since the RRI in Jelovica was significantly higher than the RRI in Trnovo and Leskova dolina. Spruce had the highest recruitment rate in Jelovica and Leskova dolina, beech had the highest recruitment rate in Trnovo, whilst fir had a significantly lower RRI than the other main tree species in all three study areas.

Silver fir underwent the most large-scale changes among the dominant tree species. The analysis of the dbh structure of fir showed two countervailing dynamics. Currently the fir population in the Alps is “younger” (i.e. higher portion of small-diameter trees) than it was at the beginning of the observation period, but in contrast, the fir population in the Dinaric Mountains was noticeably “younger” a century ago than it is today. In the alpine fir-beech forests (Jelovica), an increase in the number of small-diameter fir by 4.2 times was recorded in 1899-2002, while in the Dinaric Mountains (Leskova dolina), the quantity of large-diameter fir increased by 12.7 times from 1912 to 2004. An excess of mortality rate over recruitment rate reduced the fir proportion in tree species composition of fir-beech forests in the studied period, insignificantly in the Alps and significantly in the Dinaric Mountains.

The observed dynamics of the studied forest stands was underpinned by the complexity of natural and mainly anthropogenic factors which work at different spatiotemporal scales. Differences in past forest management, regimes of abiotic and biotic natural disturbances, and site conditions seem to be the most important impact factors in the long-term dynamics of fir-beech forest stands in Slovenia.

Past forest use had altered natural forest stand structure and composition to a considerable degree even before the first forest inventory was done and regular forest management started. Study areas also differed in the spatiotemporal impacts of different past forest uses, which reflected in different baseline states of studied forest stands and affected the dynamics of forest stands in the last century. In the period of regular forest management, the forest management concept was the most important influencing factor of forest stand dynamics. Observed deviations between study areas occurred mainly due to differences in the applied silvicultural systems, but differences in the regime and the importance of different natural disturbances in a particular study area have also been of considerable importance.

Large ungulates as a continuous biotic natural disturbance may play an important role in long-term forest stand dynamics. In Leskova dolina selective browsing by large herbivores, particularly red deer, had a major impact on the density and species composition of natural tree species regeneration, but especially on the more palatable tree species such as fir and sycamore. In fenced areas, the density of fir was 4.8 times higher than in non-fenced areas. These differences were even more obvious in the height classes, where fir regeneration in non-fenced areas completely disappeared above 50 cm in height, but was abundantly present in fenced areas. Similar results were obtained for sycamore. In addition, the recruitment of fir into small-diameter trees has constantly dropped over the last century. There were 190 small-diameter fir per hectare in 1912, but only 30 per hectare in 2004. However, the recruitment of fir started to decline even before the red deer density began to rapidly increase, suggesting that some additional factors other than browsing also affect fir recruitment. In other study areas, browsing pressure seems to be of much lower importance compared with Leskova dolina.

In the alpine fir-beech forests with mainly altered tree species composition, in addition to regular forest management, abiotic and biotic natural disturbances represent a relevant factor driving forest stand dynamics. Salvage cut due to natural disturbances averaged 50.3 % of the total annual cut in 1979-2010, but represented 89 % or more in the last five years of the observation period. Several stand characteristics, site conditions, and past forest management measures were found to be significantly related to natural disturbance (i.e. windthrow, snow breakage, and insect outbreaks) occurrence and severity. In the multivariate model, past natural and anthropogenic disturbances in the previous five years were the most predictable variables. Among stand characteristics, horizontal structure, developmental phase (stand type), and dbh structure were found to be the most important, while elevation, aspect, and topography were found to be the most elucidative among site conditions.

Site conditions are an important component influencing "natural" forest stand structure and composition, but their influence may significantly vary within the same forest type due to differences in microsite and mesosite conditions. They also have a significant impact on the occurrence and severity of some abiotic and biotic natural disturbances.

The dynamics of fir was underpinned by all mentioned factors with past forest management and browsing pressure playing the most important roles. It is highly likely that fir needs "a window of opportunity", a co-occurrence of appropriate environmental conditions, such as low enough densities of large ungulates, full- and partial-seed years, an accordant disturbance regime, and appropriate mature stand structure and composition, for its abundant regeneration and successful recruitment into the stand canopy.

The forest management regime was found to have a significant impact on changes in forest stands in the long-term. Therefore, the choice and application of a silvicultural system in stands of a particular forest type have to greatly consider not only "natural" forest stand dynamics found in old-growth or near-natural forests of a particular forest type, but also site conditions, current and potential "natural" stand characteristics, and long-term forest management goals. In this context, in the fir-beech forest type we suggest the application of silvicultural systems creating small-scale canopy gaps and vertically and horizontally heterogeneous forest landscape with stands of mainly uneven-aged structure. However, this recommendation should not be generalized and strictly followed. Intermediate and large-scale high-severity natural disturbances could also be mimicked in forest management, but site conditions and stand characteristics have to be strongly considered. To reduce the hazard and severity of natural disturbances, in addition to creating uneven-aged forest stands, the noticeable admixture of broadleaves in forest stands and thinning from above with early commencement and frequent return are proposed.

Additionally, forest management, together with wildlife management, seems to be the most important factor driving the dynamics of fir. Therefore, commutative and complementary acting of forest and wildlife planning and management should be considered to effectively solve the conflict between forest stand and wildlife components of the forest ecosystem and to maintain both fir and large ungulates at reasonable levels that will enable their sustainable use and conservation.

The forest ecosystem will never be static because it continuously responds to changes in its environment. Therefore, forest management should be oriented towards managing the processes in the forest ecosystem and less towards maintaining static structures. Furthermore, our goal should be a better understanding and sensible management of forest stand dynamics with all ecosystem components having equal priority in the process of forest ecosystem management.

4.2 POVZETEK

Spremembe sestojne zgradbe so sestavni del razvoja gozdnih sestojev. Trenutna zgradba in drevesna sestava gozdnih sestojev sta posledici vzajemnega delovanja rastiščnih dejavnikov, medvrstnih in znotrajvrstnih odnosov ter naravnih in antropogenih motenj. Slednje so bile najpomembnejši dejavnik razvoja gozdov zmernega podnebnega pasu v zadnjih nekaj stoletjih. Vseeno pa imajo naravne motnje pogosto pomembno dopolnilno vlogo v dinamiki gozdnih sestojev v daljšem časovnem obdobju. Poznavanje preteklega razvoja pa tudi procesov in dejavnikov, ki vplivajo nanj, je izrednega pomena za prihodnje ravnanje z gozdovi, še posebej v primeru adaptivnega sonaravnega gospodarjenja z gozdovi.

Pri proučevanju dolgotrajne dinamike gozdnih sestojev se uporablja vrsta raziskovalnih metod, ki temeljijo na različnih podatkovnih virih. Arhivski podatki iz gozdnih inventur so bili dolgo zapostavljeni vir informacij, vendar v zadnjem obdobju pridobivajo večji pomen in uporabno vrednost, saj omogočajo kvantifikacijo sprememb zgradbe in sestave gozdnih sestojev v daljšem časovnem obdobju. Poleg strukturnih sprememb sestojev tovrstni podatki omogočajo tudi raziskovanje in posledično razumevanje delovanja različnih vplivnih dejavnikov sestojne dinamike, predvsem spremenljivega režima naravnih in antropogenih motenj.

Dinamika jelovo-bukovih gozdnih sestojev ni povsem raziskana tema, slabo je raziskana predvsem njena variabilnost v geografsko dislociranih območjih. Zato so bili cilji naše raziskave: 1) s pomočjo arhivskih podatkov raziskati stoletno dinamiko zgradbe in drevesne sestave pretežno raznomernih jelovo-bukovih gozdnih sestojev in populacije jelke v prostorsko dislociranih raziskovalnih objektih, 2) identificirati glavne vplivne dejavnike in ovrednotiti njihovo vlogo v dinamiki proučevanih gozdnih sestojev in 3) analizirati vplivne dejavnike pojava in jakosti naravnih motenj v alpskih jelovo-bukovih gozdovih s spremenjeno drevesno sestavo.

Za uresničitev zastavljenih ciljev smo izbrali tri raziskovalne objekte na območju pretežno jelovo-bukovih gozdov. V raziskovalnem objektu Jelovica so večinsko zastopani predalpski jelovo-bukovi gozdovi asociacije *Homogyno sylvestris-Fagetum* Marinček et al. 1993, ki so danes pretežno zasmrečeni, gozdove v objektu Trnovo predstavljajo pretežno jelovo-bukovi gozdovi s florističnimi elementi dinarske, alpske in submediteranske flore asociacij *Omphalodo-Fagetum* var.geogr. *Saxifraga cuneifolia* (Surina 2001) in var.geogr. *Calamintha grandiflora* (Surina 2001), v raziskovalnem objektu Leskova dolina pa se večinsko pojavljajo dinarski jelovo-bukovi gozdovi asociacije *Omphalodo-Fagetum* (Tregubov 1957 *corr*.

Puncer 1980) Marinček et al. 1993.

Sestojno dinamiko smo proučevali s pomočjo GIS podatkovne zbirke, ki smo jo izdelali na podlagi arhivskih podatkov o gozdnih sestojih, zbranih v gozdnogospodarskih načrtih, in gozdnogospodarskih kart. V GIS zbirki podatkov so bili za posamezni odsek podatki prikazani za vsako inventurno obdobje. Podatke o gozdnih sestojih smo najprej pretvorili v digitalno obliko. Gozdnogospodarske karte posameznih raziskovalnih objektov za posamezna inventurna obdobja smo skenirali, georeferencirali in digitalizirali. S pomočjo prekrivanja digitaliziranih kart iz posameznih inventurnih obdobij in aktualne gozdnogospodarske karte smo pridobili grafično povezavo med nekdanjimi in današnjimi odseki in nato preračunali arhivske podatke na današnje prostorske enote (odseke). GIS podatkovna zbirka je za raziskovalni objekt Jelovica obsegala podatke o gozdnih sestojih za obdobje 1899-2002, za objekt Trnovo za obdobje 1897-2003 in za objekt Leskova dolina za obdobje 1912-2004.

Spremembe v zgradbi in sestavi gozdnih sestojev smo ovrednotili z izbranimi sestojnimi parametri in njihovimi kazalci: lesno zalogo in indeksom spremembe lesne zaloge SVI, debelinsko strukturo, diverziteto debelinske strukture z Ginijevem koeficientom GC, drevesno sestavo in vrastjo dreves preko meritvenega praga 10 cm v zadnjem inventurnem obdobju s pomočjo indeksa stopnje vrasti RRI. Vplivne dejavnike dinamike gozdnih sestojev smo identificirali in ovrednotili njihov pomen na podlagi informacij, zbranih iz tekstnih delov posameznih gozdnogospodarskih načrtov (ali njihovih prevodov), podatkov o poseku lesa na letni ravni, razčlenjenem po vzrokih poseka, in podatkov o letnih odvzemih velikih rastlinojedov in iz njih izračunanih gostot.

V zadnjem stoletju so se proučevani sestojni parametri značilno spreminjali. Spremembe so bile zaznane v debelinski strukturi, lesni zalogi, drevesni sestavi in diverziteti debelinske strukture. Med posameznimi raziskovalnimi objekti smo odkrili značilne razlike v sestojni dinamiki, vendar so bile ugotovljene tudi nekatere podobnosti.

Glavna skupna značilnost raziskovanih objektov je bilo stalno naraščanje lesne zaloge, ki je na Jelovici v obdobju 1899-2002 narasla za količnik 1,6 (iz 215 m^3 ha^{-1} na 340 m^3 ha^{-1}), na Trnovem v obdobju 1897-2003 prav tako za količnik 1,6 (iz 205 m^3 ha^{-1} na 328 m^3 ha^{-1}), v Leskovi dolini pa v obdobju 1912-2004 za količnik 2,4 (iz 197 m^3 ha^{-1} na 468 m^3 ha^{-1}). V raziskovalnih objektih se je spreminjala tudi debelinska struktura sestojev, vendar za razliko od lesne zaloge spremembe niso bile enosmerne in so se med raziskovalnimi objekti značilno razlikovale. Ugotovljene spremembe so nakazale dve različni smeri razvoja gozdnih sestojev: zvišanje povprečne sestojne gostote in količine tankega drevja (dbh=10-

29 cm) (»pomlajevanje sestojev«) na Jelovici in Trnovem ter zvišanje količine debelega drevja (dbh≥50 cm) in upad sestojne gostote (»staranje sestojev«) v Leskovi dolini. Na Jelovici se je v obdobju 1899-2002 število tankega drevja povečalo za 409 ha^{-1}, na Trnovem pa v obdobju 1931-2003 za 307 ha^{-1}. Nasprotno se je v Leskovi dolini med letoma 1912 in 2004 število tankega drevja znižalo za 171 ha^{-1}, število debelega drevja pa povečalo za 54 ha^{-1}. Med raziskovalnimi objekti smo ugotovili tudi razlike v dinamiki diverzitete debelinske strukture. V proučevanem obdobju se je v Leskovi dolini Ginijev koeficient GC zvišal za količnik 1,14, kar nakazuje trend razvoja sestojne zgradbe proti bolj raznomerni zgradbi. Na Trnovem je GC stagniral, kar kaže na manjše spremembe diverzitete debelinske strukture in stabilnost sestojnih zgradb. Na Jelovici pa se je GC v proučevanem obdobju znižal za količnik 1,6, saj so se sestoji iz prvotnih sestojev z najvišjo diverziteto debelinske strukture med raziskovalnimi objekti spremenili v sestoje z najnižjo diverziteto debelinske strukture (najbolj enomerne zgradbe) ob koncu proučevanega obdobja. V proučevanih gozdnih sestojih smo v zadnjem stoletju ugotovili tudi opazne spremembe v drevesni sestavi. Glavna splošna ugotovitev je, da sta se v zadnjih desetletjih zvišala deleža listavcev in smreke v lesni zalogi, znižal pa se je delež jelke. V posameznih inventurnih obdobjih so bile med raziskovalnimi objekti ugotovljene značilne razlike v deležih posameznih drevesnih vrst. Na Jelovici je bila v celotnem proučevanem obdobju smreka dominantna drevesna vrsta, medtem ko sta na Trnovem in v Leskovi dolini jelka in bukev izmenjaje prevladovali v lesni zalogi, vendar so fluktuacije potekale v različnih časovnih okvirih. Med raziskovalnimi objekti se je značilno razlikovala tudi vrast tankega drevja. Indeks stopnje vrasti RRI je bil na Jelovici statistično značilno višji od izračunanih RRI na Trnovem in v Leskovi dolini. Smreka je izkazovala najvišjo stopnjo vrasti na Jelovici in v Leskovi dolini, medtem ko je v sestoje na Trnovem najbolj vraščala bukev. Med glavnimi drevesnimi vrstami smo najnižjo stopnjo vrasti v vseh treh raziskovalnih objektih ugotovili za jelko.

Med glavnimi drevesnimi vrstami je jelka prestala največje spremembe debelinske strukture in obilja. Analiza sprememb debelinske strukture jelke v raziskovalnih objektih je nakazala dve nasprotni razvojni značilnosti. Trenutno je populacija jelke v proučevanih jelovo-bukovih gozdovih v Alpah razvojno mlajša (t.j. večji delež tankega drevja), kot je bila na začetku proučevanega obdobja, nasprotno pa je populacija jelke v proučevanih dinarskih jelovo-bukovih sestojih danes razvojno starejša (t.j. nižji delež tankega drevja ob hkratnem višjem deležu debelega drevja), kot je bila na začetku proučevanega obdobja. V proučevanih predalpskih jelovo-bukovih gozdovih (Jelovica) je bil v obdobju 1899-2002 evidentiran porast števila tankih jelk (dbh=10-19 cm) za količnik 4,2, medtem ko je v Leskovi dolini v obdobju 1912-2004 število debelih jelk (dbh≥50 cm) naraslo za količnik 12,7. Vrast jelke je bila najvišja v raziskovalnem objektu Jelovica (20,8 jelk ha^{-1}), medtem ko je bila na

Trnovem (0,8 ha^{-1}) in v Leskovi dolini (3,0 ha^{-1}) značilno nižja. Presežek mortalitete nad vrastjo jelke je v zadnjem stoletju znižal njen delež v drevesni sestavi proučevanih sestojev, manj v predalpskih, bistveno pa v dinarskih jelovo-bukovih gozdovih.

Ugotovljene razvojne spremembe so bile posledica vzajemnega delovanja naravnih, predvsem pa antropogenih motenj, ki delujejo na različnih prostorskih in časovnih ravneh. Razlike v pretekli rabi gozdov, režimih abiotskih in biotskih naravnih motenj in rastiščnih značilnostih so se izkazali kot najpomembnejši vplivni dejavniki dinamike jelovo-bukovih gozdnih sestojev v Sloveniji.

Pretekla raba gozdov je bistveno spremenila naravno zgradbo in drevesno sestavo sestojev že v obdobju pred prvimi gozdnimi inventurami in začetkom načrtnega urejanja gozdov in gospodarjenja z njimi. Prostorski in časovni vpliv različnih rab gozdnega prostora na zgradbo sestojev pred začetkom načrtnega gospodarjenja z gozdovi se je med raziskovalnimi objekti bistveno razlikoval, kar se je odrazilo v različnih stanjih proučevanih gozdnih sestojev na začetku raziskovalnega obdobja. V obdobju načrtnega gospodarjenja z gozdovi je koncept gospodarjenja z gozdovi (t.j. gozdnogojitveni sistem, način sečenj, ipd.) najpomembneje vplival na sestojno dinamiko proučevanih gozdov. Opažene razlike med raziskovalnimi objekti so bile predvsem posledica razlik v uporabljenih gozdnogojitvenih sistemih, vendar ne gre zanemariti tudi vpliva režima naravnih motenj.

Veliki rastlinojedi in njihovo objedanje pomladka drevesnih vrst kot kontinuirana biotska naravna motnja pogosto igra pomembno vlogo v dinamiki gozdnih sestojev. V Leskovi dolini je selektivno objedanje pomladka po velikih rastlinojedih, predvsem jelenjadi, imelo izjemen vpliv na gostoto in vrstno sestavo naravnega pomladka, predvsem za objedanje izjemno priljubljenih drevesnih vrst, kot sta jelka in gorski javor. V ograjenih površinah je bila skupna gostota jelovih mladic 4,8-krat višja kot na neograjenih površinah. Še bolj očitne razlike so bile ugotovljene pri analizi pomladka po višinskih razredih, saj je na neograjenih površinah pomladek jelke povsem izginil v višinskih razredih nad 50 cm, medtem ko je bil na ograjenih površinah zastopan v zadostnem deležu. Podobni rezultati so bili ugotovljeni za pomladek gorskega javorja. V preteklem stoletju je bil ugotovljen stalen upad števila preko meritvenega praga 10 cm vraslih jelk, saj jih je bilo v letu 1912 v povprečju na hektar registriranih 190, leta 2004 pa samo še 30. Vendar je vrast jelke začela upadati, še preden so gostote jelenjadi začele rapidno naraščati, kar nakazuje, da poleg velikih rastlinojedov na vrast jelke vplivajo tudi nekaterih drugi dejavniki. V ostalih dveh raziskovalnih objektih, Jelovici in Trnovem, veliki rastlinojedi in njihovo objedanje gozdnega pomladka očitno ne predstavljajo tako velike motnje kot v Leskovi dolini.

V pretežno zasmrečenih predalpskih jelovo-bukovih gozdovih predstavljajo abiotske in biotske naravne motnje pomemben dejavnik sestojne dinamike. V raziskovalnem objektu Jelovica je v obdobju 1979-2010 sanitarni posek zaradi različnih naravnih motenj v povprečju predstavljal 50,3 % celotnega letnega poseka. V zadnjih petih letih je bil ta delež celo vedno višji od 89 %. V raziskavi je bilo ugotovljeno, da na pojav in jakost vetrolomov, snegolomov in napadov insektov značilno vplivajo sestojne značilnosti, rastiščni dejavniki in pretekli gozdnogospodarski ukrepi. Pojava naravnih (sanitarne sečnje) in antropogenih motenj (redne sečnje) v petih letih pred obravnanim dogodkom sta bila ugotovljena kot dejavnika z najvišjima pojasnjevalnima vrednostima. Med sestojnimi značilnostmi je multivariatni model kot najpomembnejše izpostavil horizontalno zgradbo gozdov, razvojno fazo in debelinsko strukturo lesne zaloge, med rastiščnimi dejavniki pa nadmorsko višino, lego in položaj v pokrajini.

Rastiščne značilnosti so pomemben dejavnik, ki vpliva na »naravno« zgradbo in drevesno sestavo gozdnih sestojev. Značilnosti se lahko znotraj posameznega gozdnega tipa bistveno razlikujejo zaradi razlik v mikro- in mezorastiščih, kar vpliva na razlike v drevesni sestavi in zgradbi gozdnih sestojev. Rastišče je pomemben dejavnik tudi pri pojavljanju nekaterih abiotskih in biotskih naravnih motenj.

Ugotovljena dinamika populacije jelke je bila podobno posledica vzajemnega delovanja omenjenih dejavnikov. Najpomembnejša med njimi sta bila pretekla raba gozdov oziroma način gospodarjenja z gozdovi in veliki rastlinojedi, ki z objedanjem značilno vplivajo na pomlajevanje in vrast jelke. Zelo verjetno je, da jelka za obilno pomladitev, uspešno preraščanje in vraščanje v streho sestojev, ter višji delež v drevesni sestavi gozdnih sestojev potrebuje sočasnost ustreznih okoljskih in sestojnih razmer, kot so dovolj nizke gostote velikih rastinojedov, obdobja polnih ali delnih obrodov semena, ustrezen režim (naravnih ali antropogenih) motenj, ugodna sestava in zgradba odraslih sestojev.

V raziskavi smo ugotovili bistven vpliv preteklega gospodarjenja z gozdovi na spremembe v zgradbi gozdnih sestojev v daljšem časovnem obdobju. Zato je pomembno, da smo pri izbiri, uvajanju in uporabi gozdnogojitvenih sistemov pri gospodarjenju s posameznim gozdnim tipom previdni. Upoštevati moramo tako »naravno« sestojno dinamiko, ugotovljeno v pragozdovih ali gozdnih rezervatih določenega gozdnega tipa, kot rastiščne razmere, trenutne in potencialne »naravne« sestojne značilnosti in dolgoročne gozdnogojitvene in gozdnogospodarske cilje. V jelovo-bukovih gozdovih predlagamo uporabo gozdnogojitvenih sistemov, ki ustvarjajo vrzeli majhnih velikosti in posledično kreirajo vertikalno in horizontalno heterogene gozdove s pretežno raznomernimi in raznodobnimi sestojnimi zgradbami. Vendar pa predlagana usmeritev ne sme biti togo sprejeta in aplicirana v vse jelovo-bukove gozdove. V naravni dinamiki teh gozdov se občasno pojavljajo tudi naravne motnje srednjih in večjih jakosti. Tudi motnje takšnih jakosti in razsežnosti lahko posnemamo pri gospodarjenju z gozdovi, vendar moramo dosledno in korektno upoštevati rastiščne razmere in sestojne značilnosti. Za zmanjševanje tveganja pojava naravnih motenj ali vsaj znižanje njihovih jakosti v zasmrečenih predalpskih jelovo-bukovih gozdovih poleg ustvarjanja raznomernih sestojnih zgradb predlagamo še ohranjanje višjega deleža listavcev v drevesni sestavi in izbiralno redčenje, ki pa mora biti začeto dovolj zgodaj v razvoju gozdnega sestoja in se mora dovolj pogosto ponavljati.

Gospodarjenje z gozdovi in upravljanje populacij prostoživečih živali, predvsem velikih rastlinojedov, sta najpomembnejša dejavnika dinamike predvsem dinarskih jelovo-bukovih gozdnih sestojev. Da bi rešili dolgotrajen konflikt med sestojno in živalsko komponento gozdnega ekosistema je potrebno vzajemno, dopolnjujoče in usklajeno upravljanje sestojne in živalske komponente gozdnega ekosistema. Potreben je pristop, ki bo omogočil obstoj in trajnostno rabo jelke kot pomembnega gradnika jelovo-bukovih gozdov in vseh naravno prisotnih vrst velikih rastlinojedov.

Gozdni ekosistem se stalno odziva na spremembe v svojem okolju. Zato mora biti gospodarjenje z njim usmerjeno k upravljanju procesov in ne k ohranjanju statičnih "idealnih" sestojnih zgradb. Cilj upravljanja z gozdnim ekosistemom mora biti podrobno poznavanje in razumevanje dinamike gozdnih sestojev, posledično njeno boljše in konkretnejše usmerjanje ter vzajemno obravnavanje vseh komponent gozdnega ekosistema.

5 REFERENCES

Adamič M. 1992. Red deer management (*Cervus elaphus* L.) in Republic Slovenia: the problems, recent trends and perspectives. Zbornik gozdarstva in lesarstva, 39, 47-60.

Agnolleti M., Anderson S. 2000. Methods and Approaches in Forest History. Wallingfor, CABI Publishing: 282 str.

Allison P. D. 1999. Logistic Regression Using SAS System: Theory and Application. Cary, North Carolina, SAS Institute: 304 str.

Ammer C. 1996. Impact of ungulates on structure and dynamics of natural regeneration of mixed mountain forests in the Bavarian Alps. Forest Ecology and Management, 88, 1/2: 43-53.

Angers V. A., Messier C., Beaudet M., Leduc A. 2005. Comparing composition and structure in old-growth and harvested (selection and diameter-limit cuts) northern hardwood stands in Quebec. Forest Ecology and Management, 217, 2/3: 275-293.

Anić I., Vukelić J., Mikac S., Baksić D., Ugarković D. 2009. Effects of global climate change on the ecological niche of silver fir (*Abies alba* Mill.) in Croatia. Šumarski list, 133, 3/4: 135-144.

Anko B. 1993. Vpliv motenj na gozdni ekosistem in na gospodarjenje z njim. Zbornik gozdarstva in lesarstva, 42: 85-109.

Attiwill P. M. 1994. The disturbance of forest ecosystems - the ecological basis for conservative management. Forest Ecology and Management, 63, 2/3: 247-300.

Axelsson A. L., Östlund L., Hellberg E. 2002. Changes in mixed deciduous forests of boreal Sweden 1866-1999 based on interpretation of historical records. Landscape Ecology, 17, 5: 403-418.

Axelsson A.-L., Östlund L. 2001. Retrospective gap analysis in a Swedish boreal forest landscape using historical data. Forest Ecology and Management, 147, 2/3: 109-122.

Bachmann P., Dvorak L. 2005. Sturmschäden in Abhängigkeit vom Bestandesaufbau in einem Plenterwaldgebiet. V: LOTHAR Ursächliche Zussammenhänge und Risikoentwicklung. Synthese des Teilprogramms 6. Umwelt-Materialen Nr.184. M. Indermühle, P. Raetz, R. Volz (ur.). Bern, Swiss, Bundesamt für Umwelt, Wald und Landschaft: 51-59.

Bernadzki E., Bolibok L., Brzeziecki B., Zajaczkowski J., Zybura H. 1998. Compositional dynamics of natural forests in the Białowieza National Park, Northeastern Poland. Journal of Vegetation Science, 9, 2: 229-238.

Bernik R. 1966. Katastrofe v gozdovih triglavskega gozdnogospodarskega območja. Gozdarski vestnik, 24: 270-273.

Bigler C., Gričar J., Bugmann H., Čufar K. 2004. Growth patterns as indicators of impending tree death in silver fir. Forest Ecology and Management, 199, 2/3: 183-190.

Biolley H. 1920. L'aménagement des forêts par la méthode expérimentale et spécialement la méthode du contrôle. Neuchatel, Paris Attinger frères: 91 str.

Bleiweis S. 1983. Pogostnost in obseg škod zaradi ujm v slovenskih gozdovih. Gozdarski vestnik, 41, 6: 233-249.

Bodin P., Wiman B. L. B. 2007. The usefulness of stability concepts in forest management when coping with increasing climate uncertainties. Forest Ecology and Management, 242, 2/3: 541-552.

Bončina A. 1996. Vpliv jelenjadi in srnjadi na potek gozdne sukcesije v gozdnem rezervatu Pugled-Žiben. Gozdarski vestnik, 54, 1: 57-65.

Bončina A. 1999. Stand dynamics of the virgin forest Rajhenavski Rog (Slovenia) during the past century. V: Virgin forests and forest reserves in Central and East European countries: history, present status and future development: proceedings of the invited lecturers' reports presented at the COST E4 management committee and working groups meeting in Ljubljana, Slovenia. J. Diaci (ur.). Ljubljana, Biotechnical faculty, Department for forestry and Renewable Forest Resources: 95-110.

Bončina A. 2000. Comparison of structure and biodiversity in the Rajhenav virgin forest remnant and managed forest in the Dinaric region of Slovenia. Global Ecology & Biogeography, 9, 3: 201-211.

Bončina A. 2008. Adaptivno upravljanje z gozdovi: aktualni vidiki in perspektive. Gozdarski vestnik, 66, 7/8: 339-347.

Bončina A. 2009. Urejanje gozdov - Upravljanje gozdnih ekosistemov. Ljubljana, Biotehniška fakulteta, Oddelek za gozdarstvo in obnovljive gozdne vire: 359 str.

Bončina A., Diaci J., Cencič L. 2002. Comparison of the two main types of selection forests in Slovenia: distribution, site conditions, stand structure, regeneration and management. Forestry, 75, 4: 365-373.

Bončina A., Ficko A., Klopčič M., Matijašić D., Poljanec A. 2009. Gospodarjenje z jelko v Sloveniji. Zbornik gozdarstva in lesarstva, 90: 43-56.

Bončina A., Gašperšič F., Diaci J. 2003. Long-term changes in tree species composition in the Dinaric mountain forests of Slovenia. Forestry Chronicle, 79, 2: 227-232.

Bončina A., Robič D., Mikulič V. 2001. Standort, Struktur und Funktion slowenischer Wälder im Höchengradienten. Schweizerische Zeitschrift für Forstwessen, 152: 43-51.

Boyce M. S., Haney A. 1997. Ecosystem Management: Applications for Sustainable Forest and Wildlife Resources. New Haven, CT and London, Yale University Press: 361 str.

Brang P. 2005. Standortseinflüsse: Bodenversauerung, Wurzelsystem und Sturmschaden. V: LOTHAR - Ursächliche Zussammenhänge und Risikoentwicklung. Synthese des Teilprogramms 6. Umwelt-Materialen Nr. 184. M. Indermühle, P. Raetz, R. Volz (ur.). Bern, Bundesamt für Umwelt, Wald und Landschaft: 69-77.

Brang P., Schönenberger W., Ott E., Gardner R. H. 2001. Forests as protection from natural hazards. V: The Forests Handbook. J. Evans (ur.). Oxford, Blackwell Science: 53-81.

Brassel P., Brändli U.-B. 1999. Schweizerische Landesforstinventar. Ergebnisse der Zweitaufnahme 1993–1995. Birmensdorf, Verlag Paul Haupt, WSL, BUWAL.

Bürgi M. 1999. A case study of forest change in the Swiss lowlands. Landscape Ecology, 14: 567-575.

Cain M. D., Shelton M. G. 2001. Natural loblolly and shortleaf pine productivity through 53 years of management under four reproduction cutting methods. Southern Journal of Applied Forestry, 25, 1: 7-16.

Cameron A. D. 2002. Importance of early selective thinning in the development of long-term stand stability and improved log quality: a review. Forestry, 75, 1: 25-35.

Canham C. D., Papaik M. J., Latty E. F. 2001. Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. Canadian Journal of Forest Research, 31, 1: 1-10.

Čavlović J. 2000. Novi program gospodarjenja za G.J. "Belevine" (2000-2009) - zaustavljanje neponovljivih trendova i iniciranje povoljnih procesa u "razvoju" preborne šume? Šumarski list, 124, 7/8: 450-457.

Čavlović J., Božić M., Bončina A. 2006. Stand structure of an uneven-aged fir–beech forest with an irregular diameter structure: modeling the development of the Belevine forest, Croatia. European Journal of Forest Research, 125, 4: 325-333.

Chapman R. A., Heitzman E., Shelton M. G. 2006. Long-term changes in forest structure and species composition of an upland oak forest in Arkansas. Forest Ecology and Management, 236, 1: 85-92.

Christensen N. L., Bartuska A. M., Brown J. H., Carpenter S., D'Antonio C., Francis R., Franklin J. F., MacMahon J. A., Noss R. F., Parsons D. J., Peterson C. H., Turner M. G., Woodmansee R. G. 1996. The Report of the Ecological Society of America Committee on the Scientific Basis for Ecosystem Management. Ecological Applications, 6, 3: 665-691.

Dale V. H., Joyce L. A., McNulty S., Neilson R. P., Ayres M. P., Flannigan M. D., Hanson P. J., Irland L. C., Lugo A. E., Peterson C. J., Simberloff D., Swanson F. J., Stocks B. J., Wotton B. M. 2001. Climate change and forest disturbances. Bioscience, 51, 9: 723-734.

Deanković T. 1969. Snegolomi v Julijskih Alpah in njihovi vzroki. Gozdarski vestnik, 27, 9: 223-236.

Debeljak M., Džeroski S., Adamič M. 1999. Interactions among the red deer (*Cervus elaphus* L.) population, meteorological parameters and new growth of the natural regenerated forest in Sneznik, Slovenia. Ecological Modelling, 121, 1: 51-61.

Diaci J. 2006. Gojenje gozdov: pragozdovi, sestoji, zvrsti, načrtovanje, izbrana poglavja. Ljubljana, Biotehniška fakulteta, Oddelek za gozdarstvo in obnovljive gozdne vire: 348 str.

Diaci J., McConnell S. 1996. Sonaravno gospodarjenje z gozdovi in gospodarjenje z ekosistemi. Zbornik gozdarstva in lesarstva, 49: 105-127.

Diaci J., Rozenbergar D., Bončina A. 2010. Stand dynamics of Dinaric old-growth forest in Slovenia: are indirect human influences relevant? Plant Biosystems, 144, 1: 194-201.

Diaci J., Roženbergar D., Nagel T. A. 2010. Coexistence of silver fir and beech in the Dinaric Alps: implications for conservation and management of silver fir. Zbornik gozdarstva in lesarstva, 91: 59-74.

Dixon P. M., Weiner J., Mitchell-Olds T., Woodley R. 1987. Bootstrapping the Gini coefficient of inequality. Ecology, 68, 5: 1548-1551.

Dobbertin M. 2002. Influence of stand structure and site factors on wind damage comparing the storms Vivian and Lothar. Forest, Snow and Landscape Research, 77, 1/2: 187-205.

Dobbertin M. 2005. Erfassung der Bestandesdaten und Schäden auf dem repräsentativen 4×4-km Sanasilva-Netz. V: LOTHAR Ursächliche Zusammenhänge und Risikoentwicklung. Synthese des Teilprogramms 6. Umwelt-Materialien Nr. 184. M. Indermühle, P. Raetz, R. Volz (ur.). Bern, Bundesamt für Umwelt, Wald und Landschaft: 39-50.

Dobrowolska D. 1998. Structure of silver fir (*Abies alba* Mill.) natural regeneration in the 'Jata' reserve in Poland. Forest Ecology and Management, 110, 1/3: 237-247.

Dobrowolska D., Veblen T. T. 2008. Treefall-gap structure and regeneration in mixed *Abies alba* stands in central Poland. Forest Ecology and Management, 255, 8/9: 3469-3476.

Dorland C., Tol R. S. J., Palutikof J. P. 1999. Vulnerability of the Netherlands and Northwest Europe to storm damage under climate change. Climatic Change, 43, 3: 513-535.

Duchesne L., Ouimet R., Moore J. D., Paquin R. 2005. Changes in structure and composition of maple-beech stands following sugar maple decline in Quebec, Canada. Forest Ecology and Management, 208, 1/3: 223-236.

Dvorak L., Bachmann P., Mandallaz D. 2001. Sturmschäden in ungleichförmigen Beständen. Schweizerische Zeitung für Forstwessen, 152, 11: 445-452.

EEA 2006. European Forest Types: Categories and Types for Sustainable Forest Management Reporting and Policy. (EEA Technical Report, No. 9). Copenhagen, European Environment Agency: 111 str.

Elling W., Dittmar C., Pfaffelmoser K., Rötzer T. 2009. Dendroecological assessment of the complex causes of decline and recovery of the growth of silver fir (*Abies alba* Mill.) in Southern Germany. Forest Ecology and Management, 257, 4: 1175-1187.

Evans A. M., Camp A. E., Tyrrell M. L., Riely C. C. 2007. Biotic and abiotic influences on wind disturbance in forests of NW Pennsylvania, USA. Forest Ecology and Management, 245, 1/3: 44-53.

Fabjan I. 1956. Snežniška jelenjad. Lovec, 39, 6: 161-169.

Ferlin F. 2002. The growth potential of understorey silver fir and Norway spruce for uneven-aged forest management in Slovenia. Forestry, 75, 4: 375-383.

Ficko A., Bončina A. 2006. Silver fir (*Abies alba* Mill.) distribution in Slovenian forests. Zbornik gozdarstva in lesarstva, 79: 19-35.

Ficko A., Poljanec A., Boncina A. 2011. Do changes in spatial distribution, structure and abundance of silver fir (*Abies alba* Mill.) indicate its decline? Forest Ecology and Management, 261, 4: 844-854.

Firm D., Nagel T. A., Diaci J. 2009. Disturbance history and dynamics of an old-growth mixed species mountain forest in the Slovenian Alps. Forest Ecology and Management, 257, 9: 1893-1901.

Flamek F. 1771. Holz-Schätz oder Überschlagung auch Geometrische Einteilung in die Stallungen oder Järliche Gehausammentlicher Ternovaner Landesfürstlichen Hoch und Schwartz Waldungen.

FMP Bled 2003. Gozdnogospodarski načrt za gozdnogospodarsko območje Bled 2001-2010. = [Forest management plan GGO Bled 2001-2010]. Bled, Zavod za gozdove Slovenije, Območna enota Bled.

FMP Jelovica 1899. Forst und Verwaltung. K.k. Wirtschaftsbezirk: Radmansdorf. Religionsfondforste. Betriebs-Einrichtungs-Operat vom Jahre 1899.

FMP Jelovica 1906. Forst- u. Domanen Verwaltung. K.k. Forstwirtschaftsbezirk: Radmansdorf. Staatforst Jlovca. Revisions Operat für das Jahrzehnt 1906-1915.

FMP Jelovica 1908. Forst- u. Domanen Direktion. K.k. Forstwirtschaftsbezirk Radmannsdorf. Religionsfondforste. Revisions Operat für das Jahrzehnt 1908-1917.

FMP Jelovica 1921. Šumska uprava Bohinjska Bistrica. Državni gozd Jelovca. Revizijska osnova za petletje 1921-1925.

FMP Jelovica 1922. Šumska uprava Bohinjska Bistrica (Verski zaklad). Revizijski operat za desetletje 1922-1931.

FMP Jelovica 1927. Bohinjska Bistrica. Državni gozd Jelovca. Revizijski operat 1927-1936.

FMP Jelovica 1932. Šumska uprava Bohinjska Bistrica. Revizijski operat za desetletje 1932-1941.

FMP Jelovica 1937. Bohinjska Bistrica. Državni gozd Jelovca-Martinček. Revizijski operat za desetletje 1937-1946.

FMP Jelovica 1955. Gozdnogospodarski načrt 1955-1964. Gospodarska enota Bohinjska Bistrica. Bled, Gozdno gospodarstvo Bled /Kranj/.

FMP Jelovica 1965. Gozdnogospodarski načrt 1965-1974. Gospodarska enota Bohinjska Bistrica. Bled, Gozdno gospodarstvo Bled /Kranj/.

FMP Jelovica 1973. Gozdnogospodarski načrt 1973-1982. Gospodarska enota Jelovica. Bled, Gozdno gospodarstvo Bled /Kranj/.

FMP Jelovica 1983. Gozdnogospodarski načrt 1983-1992. Gospodarska enota Jelovica. Bled, Gozdno gospodarstvo Bled /Kranj/.

FMP Jelovica 1992. Gozdnogospodarski načrt za gozdnogospodarsko enoto Jelovica 1992-2001. Bled, Zavod za gozdove Slovenije, Območna enota Bled.

FMP Jelovica 2002. Gozdnogospodarski načrt za gozdnogospodarsko enoto Jelovica 2002-2011. Bled, Zavod za gozdove Slovenije, Območna enota Bled.

FMP Leskova dolina 1912. Betriebseinrichtung für das Dezennium 1912-1921. Reviere Schneeberg, Leskova dolina, Masun, Georgstal.

FMP Leskova dolina 1936. = [Gozdnogospodarski načrt za gozdnogospodarsko enoto Leskova dolina 1936]: 1 mapa (in Italian).

FMP Leskova dolina 1954. Gozdnogospodarski načrt revirja Leskova dolina za ureditveno obdobje 1. 1. 1954 - 31. 12. 1963. Postojna, Gozdno gospodarstvo Postojna, Sekcija za urejanje gozdov.

FMP Leskova dolina 1964. Gozdnogospodarski načrt revirja Leskova dolina za ureditveno obdobje 1964-1973. Postojna, Gozdno gospodarstvo Postojna, Sekcija za urejanje gozdov.

FMP Leskova dolina 1974. Gozdnogospodarski načrt revirja Leskova dolina za ureditveno obdobje 1974-1983. Postojna, Gozdno gospodarstvo Postojna, Sekcija za urejanje gozdov.

FMP Leskova dolina 1984. Gozdnogospodarski načrt revirja Leskova dolina za ureditveno obdobje 1984-1993. Postojna, Gozdno gospodarstvo Postojna, Sekcija za urejanje gozdov.

FMP Leskova dolina 1994. Gozdnogospodarski načrt za gozdnogospodarsko enoto Leskova dolina 1994-2003. Postojna, Zavod za gozdove Slovenije, Območna enota Postojna.

FMP Leskova dolina 2004. Gozdnogospodarski načrt za gozdnogospodarsko enoto Leskova dolina 2004-2013. Postojna, Zavod za gozdove Slovenije, Območna enota Postojna.

FMP Notranji Bohinj 1973. Gozdnogospodarski načrt 1973-1982. Gospodarska enota Notranji Bohinj. Bled, Gozdno gospodarstvo Bled /Kranj/.

FMP Notranji Bohinj 1983. Gozdnogospodarski načrt 1983-1992. Gospodarska enota Notranji Bohinj. Bled, Gozdno gospodarstvo Bled /Kranj/.

FMP Notranji Bohinj 1993. Gozdnogospodarski načrt za gozdnogospodarsko enoto Notranji Bohinj1993-2002. Bled, Zavod za gozdove Slovenije, Območna enota Bled.

FMP Notranji Bohinj 2003. Gozdnogospodarski načrt za gozdnogospodarsko enoto Notranji Bohinj 2003-2012. Bled, Zavod za gozdove Slovenije, Območna enota Bled.

FMP Trnovo 1887. Wbz. Ternova Betriebseinrichtungs - Revisions-Operat II. dec. 1887-1896.

FMP Trnovo 1897a. K.K. Wirtschaftsbezirk: Ternova. Revisions-Operat vom Jahre 1897. Ackerbau Ministerium.

FMP Trnovo 1897b. K.K. Wirtschaftsbezirk: Ternova und Dol. Revisions-Grundlagen-Protokoll 1897. Ackerbau Ministerium.

FMP Trnovo 1907. K.K. Forstwirtschaftsbezirk: Ternova. Revisions Operat für das Jahrzehnt 1907-1916. K.K. Ackerbauministerium.

FMP Trnovo 1931. Foresta di Tarnova. Piano di assestamento per il decennio 1931-1940. Azienda foreste demaniali.

FMP Trnovo 1952. Ureditveni elaborat gospodarske enote Trnovo 1952/1961. Tolmin, Soško gozdno gospodarstvo.

FMP Trnovo 1963. Ureditveni elaborat gospodarske enote Trnovo 1963-1972. Tolmin, Soško gozdno gospodarstvo.

FMP Trnovo 1973. Ureditveni elaborat gospodarske enote Trnovo 1973-1982. Tolmin, Soško gozdno gospodarstvo.

FMP Trnovo 1983. Ureditveni elaborat gospodarske enote Trnovo 1983-1992. Tolmin, Soško gozdno gospodarstvo.

FMP Trnovo 1993. Gozdnogospodarski načrt za gozdnogospodarsko enoto Trnovo 1993-2002. Tolmin, Zavod za gozdove Slovenije, Območna enota Tolmin.

FMP Trnovo 2003. Gozdnogospodarski načrt za gozdnogospodarsko enoto Trnovo 2003-2012. Tolmin, Zavod za gozdove Slovenije, Območna enota Tolmin.

Franklin J. F. 1993. The fundamentals of ecosystem management with applications in the Pacific Northwest. V: Defining Sustainable Forestry. G. H. Applet, N. Johnson, J. T. Olson, V. A. Sample (ur.). Washington, DC, Island Press: 127-144.

Frelich L. E. 2002. Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen-Deciduous Forests. Cambridge, Cambridge University Press: 266 str.

Frelich L. E., Lorimer C. G. 1985. Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. Biological Conservation, 34, 2: 99-120.

Fuhrer J., Beniston M., Fischlin A., Frei C., Goyette S., Jasper K., Pfister C. 2006. Climate risks and their impact on agriculture and forests in Switzerland. Climatic Change, 79, 1: 79-102.

Gardiner B. A., Quine C. P. 2000. Management of forests to reduce the risk of abiotic damage - a review with particular reference to the effects of strong winds. Forest Ecology and Management, 135: 261-277.

Gartner A., Papler-Lampe V., Poljanec A., Bončina A. 2007. Upoštevanje katastrof pri načrtovanju in gospodarjenju z gozdovi na primeru vetroloma na Jelovici V: Podnebne spremembe: vpliv na gozd in gozdarstvo. M. Jurc (ur.). Ljubljana, Univerza v Ljubljani, Biotehniška fakulteta, Oddelek za gozdarstvo in obnovljive gozdne vire: 153-176.

Gašperšič F. 1967. Razvojna dinamika mešanih gozdov jelke-bukve na Snežniku v zadnjih sto letih. Gozdarski vestnik, 25, 7/8: 202-237.

Gašperšič F. 1974. Zakonitosti naravnega pomlajevanje jelovo-bukovih gozdov na visokem krasu Snežniško-Javorniškega masiva: doktorska disertacija. Ljubljana: 133 str.

Genries A., Morin X., Chauchard S., Carcaillet C. 2009. The function of surface fires in the dynamics and structure of a formerly grazed old subalpine forest. Journal of Ecology, 97, 4: 728-741.

Gilbert M., Nageleisen L. M., Franklin A., Gregoire J. C. 2005. Post-storm surveys reveal large-scale spatial patterns and influences of site factors, forest structure and diversity in endemic bark-beetle populations. Landscape Ecology, 20, 1: 35-49.

Gill R. M. A. 1992a. A review of damage by mammals in north temperate forests: 1: Deer. Forestry, 65, 2: 145-169.

Gill R. M. A. 1992b. A review of damage by mammals in north temperate forests: 3: Impact on trees and forests. Forestry, 65, 4: 363-388.

Gregorčič G., Gregorčič B., Bertalanič R. 2002. Nevarni viharni vetrovi z juga. Delo 44, 289: Znanost, 16. 12. 2002: 8-9.

Guisan A., Zimmermann N. 2000. Predictive habitat distribution models in ecology. Ecological Modelling, 135, 2/3: 147-186.

Hanewinkel M. 2005. Neural networks for assessing the risk of windthrow on the forest division level: a case study in southwest Germany. European Journal of Forest Research, 124, 3: 243-249.

Hanewinkel M., Breidenbach J., Neeff T., Kublin E. 2008. Seventy-seven years of natural disturbances in a mountain forest area — the influence of storm, snow, and insect damage analysed with a long-term time series. Canadian Journal of Forest Research, 38, 8: 2249-2261.

Hanewinkel M., Zhou W. C., Schill C. 2004. A neural network approach to identify forest stands susceptible to wind damage. Forest Ecology and Management, 196, 2/3: 227-243.

Heuze P., Schnitzler A., Klein F. 2005. Consequences of increased deer browsing winter on silver fir and spruce regeneration in the Southern Vosges mountains: Implications for forest management. Annals of Forest Science, 62, 2: 175-181.

Hladnik D. 1991. Spremljanje razvoja sestojev in časovna dinamika propadanja dreves v jelovo-bukovem gozdu. Zbornik gozdarstva in lesarstva, 38: 55-96.

Hockenjos W. 2008. Tannenbäume - Eine Zukunft für *Abies alba*. Leinfelden-Echterdingen, DRW-Verlag Weinbrenner: 231 str.

Hollander M., Wolfe D. A. 1999. Non-parametric Statistical Methods. 2nd ed. New York, Wiley.

Hosmer D. W., Lemeshow S. 2000. Applied Logistic Regression. 2nd ed. New York, John Wiley & Sons.

Hufnagl L. 1893. Der Plenterwald, sein Normalbild, Holzvorrat, Zuwachs und Ertrag. Österreichische Vierteljahresschrift für Forstwesen, 117-132.

Jakša J., Kolšek M. 2010. Naravne ujme v slovenskih gozdovih. V: Naravne nesreče: od razumevanja do upravljanja. M. Zorn, B. Komac, M. Pavšek, P. Pagon (ur.). Ljubljana, Založba ZRC: 39-48.

Jalkanen A., Mattila U. 2000. Logistic regression models for wind and snow damage in northern Finland based on the National Forest Inventory data. Forest Ecology and Management, 135, 1/3: 315-330.

Jarni K., Robic D., Boncina A. 2004. Analysis of the influence of ungulates on the regeneration of Dinaric fir-beech forests in the research site Trnovec in the Kočevje forest management region. Zbornik gozdarstva in lesarstva, 74: 141-164.

Jerina K. 2006. Prostorska razporeditev, območja aktivnosti in telesna masa jelenjadi (*Cervus elaphus* L.) glede na okoljske dejavnike: doktorska disertacija. Ljubljana: 172

str.

Jerina K. 2008. Velika rastlinojeda divjad in razvojna dinamika gozdnih ekosistemov: proučevanje vplivov izbranih okoljskih in populacijskih parametrov ter gozdnogojitvenih sistemov na zmožnosti naravne obnove: zaključno poročilo o rezultatih opravljenega raziskovalnega dela na projektu v okviru ciljnega raziskovalnega projekta (CRP) "Konkurenčnost Slovenije 2006-2013". Ljubljana, Biotehniška fakulteta, Oddelek za gozdarstvo in obnovljive gozdne vire: 27 str.

Johann E. 2006. Historical development of nature-based forestry in Central Europe. V: Nature-based forestry in Central Europe: alternatives to industrial forestry and strict preservation. J. Diaci (ur.). Ljubljana, Biotehniška fakulteta, Oddelek za gozdarstvo in obnovljive gozdne vire: 1-18.

Johann E. 2007. Traditional forest management under the influence of science and industry: The story of the alpine cultural landscapes. Forest Ecology and Management, 249, 1/2: 54-62.

Jørgensen S. E., Bendoricchio G. 2001. Fundamentals of Ecological Modelling. 3rd ed. Amsterdam, Elsevier: 530 str.

Kilpeläinen A., Gregow H., Strandman H., Kellomäki S., Venäläinen A., Peltola H. 2010. Impacts of climate change on the risk of snow-induced forest damage in Finland. Climatic Change, 99, 1: 193-209.

Klopčič M., Bončina A. 2010. Dynamics of silver fir (*Abies alba* Mill.)-European beech (*Fagus sylvatica* L.) forests in the period 1899-2002. V: Mixed and pure forests in a changing world : IUFRO conference 2010, 6-8 October: book of abstracts. Vila Real, Portugal. Lopez, D. et al. (ur.). Vila Real, Portugal, University of Trás-os-Montes e Alto Douro.

Klopčič, M., Bončina, A. 2011. Stand dynamics of silver fir (*Abies alba* Mill.)-European beech (*Fagus sylvatica* L.) forests during the past century: a decline of silver fir? Forestry, (in press).

Klopčič M., Diaci J. 2008. Gap characteristics and development of regeneration following a blowdown in the old-growth forest remnant Pečka. Glasnik za šumske pokuse, 42: 43-56.

Klopčič M., Jerina K., Bončina A. 2010. Long-term changes of structure and tree species composition in Dinaric uneven-aged forests: are red deer an important factor? European Journal of Forest Research, 129, 3: 277-288.

Klopčič M., Poljanec A., Gartner A., Bončina A. 2009. Factors related to natural disturbances in mountain Norway spruce (*Picea abies*) forests in the Julian Alps. Ecoscience, 16, 1: 48-57.

Knoke T., Ammer C., Stimm B., Mosandl R. 2008. Admixing broadleaved to coniferous tree species: a review on yield, ecological stability and economics. European Journal of Forest Research, 127, 2: 89-101.

König A. 1995. Sturmgefährdung von Beständen im Alterklassenwald. Frankfurt am Main, J.D. Sauerländer's Verlag.

Kordiš F. 1993. Dinarski jelovo bukovi gozdovi v Sloveniji. Ljubljana, Biotehniška fakulteta, Oddelek za gozdarstvo in obnovljive gozdne vire: 139 str.

Koren I. 1997. Vpliv rastlinojede divjadi na pomladitveni potencial gozdov zahodnega visokega krasa. Gozdarski vestnik, 55, 2: 97-109.

Korpel S. 1995. Die Urwälder der Westkarpaten. Stuttgart, Gustav Fisher Verlag: 310 str.

Kotar M. 2005. Zgradba, rast in donos gozda na ekoloških in fizioloških osnovah. Ljubljana, Zveza gozdarskih društev Slovenije, Zavod za gozdove Slovenije: 500 str.

Kovač M., Kušar G., Hočevar M., Simončič P., Poljanec A., Skudnik M., Šturm T., Gartner A., Kozorog E. 2009. Kontrolna vzorčna metoda v Sloveniji - zgodovina, značilnosti in uporaba. Ljubljana, Gozdarski inštitut Slovenije, Silva Slovenica: 104 str.

Kramer M. G., Hansen A. J., Taper M. L., Kissinger E. J. 2001. Abiotic controls on long-term windthrow disturbance and temperate rain forest dynamics in southeast Alaska. Ecology, 82, 10: 2749-2768.

Kräuchi N., Brang P., Schonenberger W. 2000. Forests of mountainous regions: gaps in knowledge and research needs. Forest Ecology and Management, 132, 1: 73-82.

Krofel M., Kos I., Linnel J., Odden J., Teurlings I. 2008. Human kleptoparasitism on Eurasian lynx (*Lynx lynx* L.) in Slovenia and Norway. Varstvo narave, 21: 93-103.

Larsen J. B. 1986. Silver fir decline - A new hypothesis concerning this complex decline syndrome in *Abies alba* (Mill). Forstwissenschaftliches Centralblatt, 105, 5: 381-396.

Larsen J. B. 1995. Ecological stability of forests and sustainable silviculture. Forest Ecology and Management, 73, 1/3: 85-96.

Leak W. B., Filip S. M. 1977. Thirty-eight years of group selection in New England northern hardwoods. Journal of Forestry, 75, 10: 641-643.

Lexerød N. L., Eid T. 2006. An evaluation of different diameter diversity indices based on criteria related to forest management planning. Forest Ecology and Management, 222, 1/3: 17-28.

Linder P. 1998. Structural changes in two virgin boreal forest stands in central Sweden over 72 years. Scandinavian Journal of Forest Research, 13, 4: 451-461.

Linder P., Östlund L. 1998. Structural changes in three mid-boreal Swedish forest landscapes, 1885-1996. Biological Conservation, 85, 1/2: 9-19.

Lindner M., Maroschek M., Netherer S., Kremer A., Barbati A., Garcia-Gonzalo J., Seidl R., Delzon S., Corona P., Kolström M., Lexer M. J., Marchetti M. 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. Forest Ecology and Management, 259: 698-709.

Lorimer C. G., White A. S. 2003. Scale and frequency of natural disturbances in the northeastern US: implications for early successional forest habitats and regional age distributions. Forest Ecology and Management, 185, 1/2: 41-64.

Maarel v. d. E. 2005. Vegetation ecology. Malden, Blackwell: 395 str.

Mason W. L. 2002. Are irregular stands more windfirm? Forestry, 75, 4: 347-355.

Mayer P., Brang P., Dobbertin M., Hallenbarter D., Renaud J.-P., Walthert L., Zimmermann S. 2005. Forest storm damage is more frequent on acidic soils. Annals of Forest Science, 62, 4: 303-311.

Minami M. 2000. Using ArcMap. GIS by ESRI. New York, Environmental Systems Research Institute: 528 str.

Montes F., Sánchez M., Río M. d., Cañellas I. 2005. Using historic management records to characterize the effects of management on the structural diversity of forests. Forest Ecology and Management, 207, 1/2: 279-293.

Moore P. D., Webb J. A., Collinson M. E. 1997. Pollen analysis. London, Blackwell: 216 str.

Mosandl R., Felbermeier B. 1999. Auf dem Weg zum naturnahen Wald. AFZ/Der Wald, 17: 910-914.

Motta R. 1996. Impact of wild ungulates on forest regeneration and tree composition of mountain forests in the Western Italian Alps. Forest Ecology and Management, 88, 1/2: 93-98.

Motta R., Garbarino F. 2003. Stand history and its consequences for the present and future dynamic in two silver fir (*Abies alba* Mill.) stands in the high Pesio Valley (Piedmont, Italy). Annals of Forest Science, 60, 4: 361-370.

Nagel T., Svoboda M., Rugani T., Diaci J. 2010. Gap regeneration and replacement patterns in an old-growth *Fagus–Abies* forest of Bosnia–Herzegovina. Plant Ecology, 208, 2: 307-318.

Nagel T. A., Diaci J. 2006. Intermediate wind disturbance in an old-growth beech-fir forest in southeastern Slovenia. Canadian Journal of Forest Research, 36, 3: 629-638.

Nagel T. A., Levanic T., Diaci J. 2007. A dendroecological reconstruction of disturbance in an old-growth *Fagus-Abies* forest in Slovenia. Annals of Forest Science, 64, 8: 891-897.

Nagel T. A., Svoboda M. 2008. Gap disturbance regime in an old-growth *Fagus-Abies* forest in the Dinaric Mountains, Bosnia-Herzegovina. Canadian Journal of Forest Research, 38, 11: 2728-2737.

Nagel T. A., Svoboda M., Diaci J. 2006. Regeneration patterns after intermediate wind disturbance in an old-growth *Fagus-Abies* forest in southeastern Slovenia. Forest Ecology and Management, 226, 1/3: 268-278.

Nilsson C., Stjernquist I., Barring L., Schlyter P., Jonsson A. M., Samuelsson H. 2004. Recorded storm damage in Swedish forests 1901-2000. Forest Ecology and Management, 199, 1: 165-173.

Nykänen M.-L., Peltola H., Quine C., Kellomäki S., Broadgate M. 1997. Factors affecting snow damage of trees with particular reference to European conditions. Silva Fennica, 31, 2: 193-213.

Oberdorfer E. 2001. Pflanzensoziologische Exkursionsflora für Deutschland und angrenzende Gebiete: 8. Aufluge. Stutgart, Eugen Ulmer Gmbh & Co.: 1051 str.

Ogris N., Džeroski S., Jurc M. 2004. Windthrow factors - a case study on Pokljuka. Zbornik gozdarstva in lesarstva, 74: 59-76.

O'Hara K. L., Hasenauer H., Kindermann G. 2007. Sustainability in multi-aged stands: an analysis of long-term plenter systems. Forestry, 80, 2: 163-181.

Oliver C. D., Larsen B. C. 1996. Forest Stand Dynamics. New York, Wiley: 520 str.

Ott E. 1989. Verjüngungsprobleme in hochstaudenreichen Gebirgsnadelwäldern. Schweizerische Zeitung für Forstwessen, 140, 1: 23-42.

Ott E., Frehner M., Frey H. U., Lüscher P. 1997. Gebirgsnadelwälder: Ein praxisorientirter Leitfaden für eine standortgerechte Waldbehandlung. Bern, Paul Haupt Verlag: 287 str.

Papež J., Černigoj V. 2007. Zgodovina gospodarjenja z gozdovi v GGE Predmeja. Gozdarski vestnik, 65, 1: 46-60.

Papler-Lampe V. 2008. Snegolom, ki je januarja 2007 prizadel blejske gozdove. Gozdarski vestnik, 66, 5/6: 309-319.

Papler-Lampe V., Kolšek M. 2009. Posledice snegoloma decembra 2008 v Gozdnogospodarskem območju Bled. Novice iz varstva gozdov, 2: 9-10.

Patil G. P., Taillie C. 1982. Diversity as a concept and its measurement. Journal of the American Statistical Association, 77, 379: 548-561.

Pellikka P., Järvenpää E. 2003. Forest stand characteristics and wind and snow induced forest damage in boreal forest. V: Proceedings of the International Conference on Wind Effects on Trees. B. Ruck (ur.). Karlsruhe, University of Karlsruhe: 269-276.

Peltonen M. 1999. Windthrows and dead-standing trees as bark beetle breeding material at forest-clearcut edge. Scandinavian Journal of Forest Research, 14, 6: 505-511.

Perko F. 2002. Zapisano v branikah: Gozdovi in gozdarstvo od Snežnika do Nanosa skozi čas. Postojna, Gozdarsko društvo Postojna: 272 str.

Petit C. C., Lambin E. F. 2002. Long-term land-cover change in the Belgian Ardennes (1775-1929): model-based reconstruction vs. historical maps. Global Change Biology, 8: 616-630.

Pfeffer A. 1995. Zentral- und westpalaearktische Borken- und Kernkaefer (*Coleoptera: Scolytidae, Platypodidae*). Basel, Pro Entomologia, c/o Naturhistorisches Museum Basel: 198 str.

Pickett S. T., White P. S. 1985. The Ecology of Natural Disturbance and Patch Dynamics. San Diego, Academic Press: 472 str.

Pielou E. C. 1975. Ecological Diversity. New York, John Wiley: 165 str.

Pintarič K. 1978. Urwald Peručica als natürliches Forschungslaboratorium. Allgemeine Forst Zeitschrift, 24: 702-707.

Poljanec A., Ficko A., Bončina A. 2010. Spatiotemporal dynamic of European beech (*Fagus sylvatica* L.) in Slovenia, 1970-2005. Forest Ecology and Management, 259, 11: 2183-2190.

Prpić B., Matić S., Vukelić J., Seletković Z. 2001. Virgin forests of beech and fir in the Croatian Dinaric Mountain range. V: Obična jela u Hrvatskoj. B. Prpić (ur.). Zagreb, Akademija šumarskih znanosti, Hrvatske šume: 479-500.

Prpić B. (ur.) 2001. Obična jela u Hrvatskoj. Zagreb, Akademija šumarskih znanosti, Hrvatske šume: 895 str.

Putman R. J. 1996. Ungulates in temperate forest ecosystems: perspectives and recommendations for future research. Forest Ecology and Management, 88, 1/2: 205-214.

Rabotnov T. A. 1992. Phytozönologie: Struktur und Dynamik natürlicher Ökosysteme. Stuttgart, Verlag Eugen Ulmer: 243 str.

Radeloff V. C., Mladenoff D. J., He H. S., Boyce M. S. 1999. Forest landscape change in the northwestern Wisconsin Pine Barrens from pre-European settlement to the present. Canadian Journal of Forest Research, 29, 11: 1649-1659.

Risch A. C., Nagel L. M., Schutz M., Krusi B. O., Kienast F., Bugmann H. 2003. Structure and long-term development of subalpine *Pinus montana* Miller and *Pinus cembra* L. forests in the Central European Alps. Forstwissenschaftliches Centralblatt, 122, 4: 219-230.

Roseberry J. L., Woolf A. 1991. A comparative evaluation of techniques for analyzing white-tailed deer harvest data. Wildlife monographs, 117.

Rottmann M. 1985. Schneebruchschäden in Nadelholzbeständen. Beiträge zur Beurteilung der Schneebruchgefährdung, zur Schadensvorbeugung und zur Behandlung schneegeschädigter Nadelholzbestände. Frankfurt am Main, J.D. Sauerlander's Verlag: 159 str.

Ruel J. C. 2000. Factors influencing windthrow in balsam fir forests: from landscape studies to individual tree studies. Forest Ecology and Management, 135, 1/3: 169-178.

Schelhaas M. J., Nabuurs G. J., Schuck A. 2003. Natural disturbances in the European forests in the 19th and 20th centuries. Global Change Biology, 9, 11: 1620-1633.

Schiesser H. H., Pfister C., Bader J. 1997. Winter storms in Switzerland North of the Alps 1864/1865–1993/1994. Theoretical and Applied Climatology, 58, 1: 1-19.

Schollmayer H. 1906. Direktiven für die Bestandesaufnahme und die Betriebseinrichtung auf der F.C. Herrschaft Schneeberg. Laibach, Kleinmayr - Bamberg: 30 str.

Schumacher S., Bugmann H. 2006. The relative importance of climatic effects, wildfires and management for future forest landscape dynamics in the Swiss Alps. Global Change Biology, 12, 8: 1435-1450.

Schuster W. S. F., Griffin K. L., Roth H., Turnbull M. H., Whitehead D., Tissue D. T. 2008. Changes in composition, structure and aboveground biomass over seventy-six years (1930-2006) in the Black Rock Forest, Hudson Highlands, southeastern New York State. Tree Physiology, 28, 4: 537-549.

Schütt P., Weisberger H., Lang U. M., Roloff A., Stimm B. 1999. Abies alba Miller, 1768. V: Enzyclopädie der Holzgewächse: Handbuch und Atlas der Dendrologie, 16. Ergänzungslieferung. P. Schütt, A. Roloff (ur.). Weinheim, Wiley-VCH.

Schütz J.-P. 2001. Der Plenterwald und weitere Formen strukturierter und gemischter Wälder. Berlin, Parey: 207 str.

Schütz J. P. 2005. Einfluss verschiedener Faktoren auf Art und Ausmass der Sturmschäden: Windcharacteristic und Sturmschäden im Raum Reusstal-Limattal. V: LOTHAR Ursächliche Zusammenhänge und Risikoentwicklung. Synthese des Teilprogramms 6. Umwelt-Materialien Nr. 184. M. Indermühle, P. Raetz, R. Volz (ur.). Bern, Bundesamt für Umwelt, Wald und Landschaft: 29-38.

Schutz J. P., Gotz M., Schmid W., Mandallaz D. 2006. Vulnerability of spruce (*Picea abies*) and beech (*Fagus sylvatica*) forest stands to storms and consequences for silviculture. European Journal of Forest Research, 125, 3: 291-302.

Schweingruber F. H. 1996. Tree rings and environment. Dendroecology. Bern, Birmensdorf, Swiss Federal Institute for Forest, Snow and Landscape Research, Paul Haupt Verlag: 609 str.

Scrinzi G., Marzullo L., Galvagni D. 2007. Development of a neural network model to update forest distribution data for managed alpine stands. Ecological Modelling, 206, 3/4: 331-346.

Seidl R., Baier P., Rammer W., Schopf A., Lexer M. J. 2007. Modelling tree mortality by bark beetle infestation in Norway spruce forests. Ecological Modelling, 206, 3/4: 383-399.

Seidl R., Fernandes P. M., Fonseca T. F., Gillet F., Jönsson A. M., Merganicová K., Netherer S., Arpaci A., Bontemps J.-D., Bugmann H., González-Olabarria J. R., Lasch P., Meredieu C., Moreira F., Schelhaas M.-J., Mohren F. 2011. Modelling natural disturbances in forest ecosystems: a review. Ecological Modelling, 222, 4: 903-924.

Sendak P. E., Brissette J. C., Frank R. M. 2003. Silviculture affects composition, growth, and, yield in mixed northern conifers: 40-year results from the Penobscot Experimental Forest. Canadian Journal of Forest Research, 33, 11: 2116-2128.

Senn J., Suter W. 2003. Ungulate browsing on silver fir (*Abies alba*) in the Swiss Alps: beliefs in search of supporting data. Forest Ecology and Management, 181, 1/2: 151-164.

Seymour R. S., White A. S., deMaynadier P. G. 2002. Natural disturbance regimes in northeastern North America - evaluating silvicultural systems using natural scales and frequencies. Forest Ecology and Management, 155, 1/3: 357-367.

Simak M. 1951. Untersuchungen über den naturlichen Bauartenwechsel in der schweizerischen Plenterwälder. Mitteilungen Eidgenosischen Anstalt für Forstlichen Versuchswessen, 27: 406-468.

Simončič T., Bončina A. 2010. Jelka v gozdovih Bohorja – posebnost v slovenskem merilu? Gozdarski vestnik, 68, 1: 3-15.

Slovenia Forest Service (SFS) 2010. TIMBER: podatkovna zbirka o poseku za obdobje 1979-2010. = (TIMBER: The database of cutting for the period 1979-2010). Ljubljana, Zavod za gozdove Slovenije.

Smith D. W., Drummer T. D., Murphy K. M., Guernsey D. S., Evans S. B. 2004. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park. Journal of Wildlife Management, 68: 153-166.

Smolej I. 1984. Prispevek k zgodovini blejskih gozdov. Kronika. Časopis za Slovensko krajevno zgodovino, 32: 145-154.

Solomon D. S., Gove J. H. 1999. Effects of uneven-age management intensity on structural diversity in two major forest types in New England. Forest Ecology and Management, 114, 2/3: 265-274.

Spiecker H. 2000. Growth of Norway spruce (*Picea abies* [L.] Karst.) under changing environmental conditions in Europe. V: Spruce monocultures in Central Europe - Problems and prospects (EFI Proceedings No. 33). E. Klimo, H. Hager, J. Kulhavý (ur.).

Spiecker H., Hansen J., Klimo E., Skovsgaard J. P., Sterba H., von Teuffel K. 2004. Norway Spruce conversion - Options and consequences. Joensuu, European Forest Institute: 269 str.

Splechtna B. E., Gratzer G. 2005. Natural disturbances in Central European forests: approaches and preliminary results from Rothwald, Austria. Forest, Snow and Landscape Research, 79, 1/2: 57-67.

Splechtna B. E., Gratzer G., Black B. A. 2005. Disturbance history of a European old-growth mixed-species forest - A spatial dendro-ecological analysis. Journal of Vegetation Science, 16, 5: 511-522.

Stancioiu P. T., O'Hara K. L. 2006. Regeneration growth in different light environments of mixed species, multiaged, mountainous forests of Romania. European Journal of Forest Research, 125, 2: 151-162.

Stathers R. J., Rollerson T. P., Mitchell S. J. 1994. Windthrow handbook for British Columbia forests (Working Paper 9401). Victoria, British Columbia, BC Ministry of Forests.

Stergar M., Jonozović M., Jerina K. 2009. Območja razširjenosti in relativne gostote avtohtonih vrst parkljarjev v Sloveniji. Gozdarski vestnik, 67, 9: 367-380.

Swetnam T. W., Allen C. D., Betancourt J. L. 1999. Applied historical ecology: using the past to manage for the future. Ecological Applications, 9, 4: 1189-1206.

Šercelj A. 1996. Začetki in razvoj gozdov v Sloveniji. Ljubljana, Slovenska akademija znanosti in umetnosti: 142 str.

Ulanova N. G. 2000. The effects of windthrow on forests at different spatial scales: a review. Forest Ecology and Management, 135, 1/3: 155-167.

Valinger E., Fridman J. 1997. Modelling probability of snow and wind damage in Scots pine stands using tree characteristics. Forest Ecology and Management, 97, 3: 215-222.

Veber I. 1986. Gozdovi bohinjskih fužinarjev. Bled, Gozdno gospodarstvo Bled: 48 str.

Veblen T. T., Hadley K. S., Nel E. M., Kitzberger T., Marion R., Villalba R. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest.

Journal of Ecology, 82, 1: 125-135.

Veselič Ž. 1991. Na Postojnskem preštevilna divjad se naprej hudo ogroža gozdno mladje. Gozdarski vestnik, 49: 147-157.

Veselič Ž., Robič D. 2001. Posodobitev poimenovanja sintaksonov, ki nakazujejo (indicirajo) skupine rastišč, njihove podskupine in rastiščne tipe v računalniški bazi CE ZGS: tipkopis. Ljubljana, Zavod za gozdove Slovenije: 27 str.

Vrska T., Adam D., Hort L., Kolár T., Janík D. 2009. European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) rotation in the Carpathians-A developmental cycle or a linear trend induced by man? Forest Ecology and Management, 258, 4: 347-356.

Webb N. F., Hebblewhite M., Merrill E. H. 2008. Statistical methods for identifying wolf kill sites using global positioning system locations. Journal of Wildlife Management, 72: 798-807.

Weiner J., Solbrig O. T. 1984. The meaning and measurement of size hierarchies in plant populations. Oecologia, 61: 334-336.

Wermelinger B. 2004. Ecology and management of the spruce bark beetle *Ips typographus* - a review of recent research. Forest Ecology and Management, 202, 1/3: 67-82.

Wermelinger B., Duelli P., Obrist M. K. 2002. Dynamics of saproxylic beetles (*Coleoptera*) in windthrow areas in alpine spruce forests. Forest, Snow and Landscape Research, 77, 1/2: 133-148.

Wick L., Mohl A. 2006. The mid-Holocene extinction of silver fir (*Abies alba*) in the Southern Alps: a consequence of forest fires? Palaeobotanical records and forest simulations. Vegetation History and Archaeobotany, 15, 4: 435-444.

Woods K. D. 2004. Intermediate disturbance in a late-successional hemlock-northern hardwood forest. Journal of Ecology, 92, 3: 464-476.

Worrall J. J., Lee T. D., Harrington T. C. 2005. Forest dynamics and agents that initiate and expand canopy gaps in *Picea–Abies* forests of Crawford Notch, New Hampshire, USA. Journal of Ecology, 93, 1: 178-190.

Wraber M. 1950. O vzrokih in posledicah vetroloma na Jelovici. Gozdarski vestnik, 8: 306-309.

Yoshida T., Noguchi M., Akibayashi Y., Noda M., Kadomatsu M., Sasa K. 2006. Twenty years of community dynamics in a mixed conifer - broad-leaved forest under a selection system in northern Japan. Canadian Journal of Forest Research, 36, 6: 1363-1375.

Zar J. H. 2010. Biostatistical Analysis. 5th edition. Upper Saddle River, New Jersey, Pearson Education International: 944 str.

Zeibig A., Diaci J., Wagner S. 2005. Gap disturbance patterns of a *Fagus sylvatica* virgin forest remnant in the mountain vegetation belt of Slovenia. Forest, Snow and Landscape Research, 79, 1/2: 69-80.

Zupančič M. 1969. Vetrolomi in snegolomi v Sloveniji v povojni dobi. Gozdarski vestnik, 27: 193-210.

ZAHVALA

Najprej bi se rad zahvalil mentorju prof. dr. Andreju Bončini, da me je sredi leta 2006 kontaktiral, mi predstavil možnost zaposlitve kot mladi raziskovalec in tako omogočil pridobitev naziva doktor znanosti. Preko usmerjanja mojega raziskovalnega dela je ključno pripomogel k objavi člankov v znanstvenih revijah in izdelavi doktorske disertacije v obliki, kakršna je sedaj. V štiri in pol letnem obdobju sem se od njega zares veliko naučil, tako na profesionalni kot na osebnostni ravni. Zahvaljujem se mu, da mi je s posredovanjem idej, stalnim spodbujanjem in zastavljanjem relativno visokih ciljev omogočil intelektualni napredek, z mnogimi debatami, sugestijami, izmenjavami mnenj pa znatno vplival tudi na moj osebnostni razvoj.

Velika zahvala za nastanek moje doktorske disertacije gre tudi ožjim sodelavcem v Skupini za urejanje gozdov in biometrijo, Alešu Poljancu, Andreju Ficku, Tini Simončič, Alešu Kaduncu in Vidi Martinčič Bravec, s katerimi smo ustvarili prijetno in prijateljsko, a hkrati delovno in ustvarjalno timsko vzdušje. Pri pridobivanju arhivskih virov podatkov in izdelavi podatkovne zbirke mi je bil v veliko pomoč Aleš Poljanec, za kar se mu najlepše zahvaljujem.

Posebej se moram zahvaliti tudi vsem soavtorjem člankov, ki so del moje doktorske disertacije. Doc. dr. Klemen Jerina je vložil veliko svojega dela, znanja in idej v naš skupen članek, za kar sem mu nadvse hvaležen. Poleg tega se mu zahvaljujem tudi za pomoč pri iskanju odgovorov na številna druga vprašanja, ki so se porajala tekom študija in izdelave disertacije.

Zahvala gre tudi zaposlenim na Zavodu za gozdove Slovenije, ki so mi omogočili izposojo arhivskega gradiva, posredovali podatke ali mi z različnimi sugestijami, debatami, mnenji pomagali izdelati doktorsko disertacijo takšno kot je. Zahvaljujem se Vidi Papler-Lampe, Andreju Gartnerju, Marku Gašperinu, Edu Kozorogu, Draganu Matijašiću, Janezu Pagonu, Igorju Pridigarju, Silvu Repincu, Janezu Šemrlu, Janezu Škerbecu in Marku Udoviču. Posebej pa se moram zahvaliti Franciju (Frenku) Cergolju, ki mi je od samega začetka pomagal pri iskanju arhivskega gradiva za gozdnogospodarski enoti Jelovica in Notranji Bohinj, pri vnosu podatkov v digitalno obliko in pri izdelavi celotne podatkovne zbirke. Njegovo poznavanje gospodarjenja z gozdovi na blejskem gozdnogospodarskem območju, še posebej na Jelovici, mi je velikokrat pomagalo pri razjasnitvi problemov.

Zahvaljujem se tudi vsem sodelavcem na Oddelku za gozdarstvo in obnovljive gozdne vire, še posebej Andreji Repe, Matiji Stergarju, Danijelu Borkoviću in Tomažu Adamiču, s katerimi smo spili precej kavic in pojedli veliko malic. O različnih temah smo pogosto debatirali tudi z gojitelji, Dejanom Firmom, Tihomirjem Ruganijem, Dušanom Roženbergarjem in Tomom A. Nagelom. Slednjemu se zahvaljujem tudi za pomoč pri nešteto prevodih in korekcijah angleških povzetkov, izvlečkov, pa tudi celih člankov.

Posebej se zahvaljujem tudi recenzentoma doc. dr. Davidu Hladniku in prof. dr. Marcu Marchettiju, ki sta mi s hitro recenzijo in oceno disertacije omogočila hiter zagovor in s tem pravočasno izpolnitev moje delovne pogodbe. Doc. dr. Hladniku se zahvaljujem tudi za

pomoč pri reševanju nekaterih problemov ob izdelavi GIS podatkovne zbirke, prof. dr. Marchettiju pa, da mi je omogočil dvotedensko bivanje na Univerzi v Molisi, na Oddelku za znanost in tehnologijo okolja in prostora v Isernii, Italija, in da je bil pripravljen sprejeti odgovornost in dodatno delo kot recenzent moje doktorske disertacije.
I would like to thank both reviewers doc. dr. David Hladnik and prof. dr. Marco Marchetti for their quick review and evaluation of my PhD thesis, which made the PhD defending possible in such a short time. I would like to thank doc. dr. David Hladnik for his help in solving particular problems when creating the GIS database. Special thanks goes also to prof. dr. Marco Marchetti, who enabled me to spend a short time at his Universita degli Studi del Molise, Dipartimento di Scienze e Technoogie per l'Ambiente e il Teritiorio and that he was prepared to take the responsibility and additional work of being the reviewer of my PhD thesis.

Za lektoriranje večine doktorske disertacije se zahvaljujem Janu Nagelu, za lektoriranje izvlečka in povzetka v slovenščini pa Mojci Grden.
I would like to thank Jan Nagel for proofreading the majority of my PhD thesis and Mojca Grden for proofreading the slovenian abstract and summary.

Zahvalil bi se tudi Agenciji za raziskovalno dejavnost Republike Slovenije, da mi je finančno omogočila podiplomski študij in nadgradnjo moje izobrazbe.

Na koncu se moram iskreno zahvaliti moji družini, ženi Idi, sinu Binetu, očetu, bratu in starim staršem, da so mi ves čas podiplomskega študija stali ob strani, me spodbujali in me polnili z energijo, ki me je pripeljala do cilja. Kot že rečeno v posvetilu, mojo doktorsko nalogo posvečam njim, še posebej pa moji mami Sonji, ki nas je žal veliko prekmalu zapustila. Mami, ves čas si mi stala ob strani, me spodbujala, ko je bilo težko, verjela vame in si želela biti zraven, ko bom zaprl to poglavje moje življenjske knjige. Žal si odšla prekmalu. Zato mojo doktorsko disertacijo v prvi vrsti posvečam tebi. Hvala, ker si bila to, kar si bila - moja mami.