

Article

Composition and Elevation of Spruce Forests Affect Susceptibility to Bark Beetle Attacks: Implications for Forest Management

Massimo Faccoli ^{1,*} and Iris Bernardinelli ²

¹ Department of Agronomy, Food, Natural resources, Animals and Environment, University of Padova, Viale dell'Università, 16/a, Legnaro 35020 PD, Italy

² Servizio fitosanitario e chimico, ricerca, sperimentazione e assistenza tecnica—ERSA, via Sabbatini 5, Pozzuolo del Friuli 33050 UD, Italy; E-Mail: iris.bernardinelli@regione.fvg.it

* Author to whom correspondence should be addressed; E-Mail: massimo.faccoli@unipd.it; Tel.: +39-049-8272891; Fax: +39-049-8272810.

Received: 13 November 2013; in revised form: 31 December 2013 / Accepted: 6 January 2014 / Published: 14 January 2014

Abstract: The spruce bark beetle, *Ips typographus* (L.) (Coleoptera: Curculionidae, Scolytinae), is one of the most destructive insects infesting spruce forests in Europe. Data concerning infestations of *I. typographus* occurring over the last 19 years (1994–2012) on the Southern Alps were analyzed in seven spruce forest types: (1) pure spruce plantations; (2) pure spruce reforestations; (3) pure spruce mountain forests; (4) pure spruce alpine forests; (5) spruce-conifer mixed forests; (6) spruce-broadleaf mixed forests; and (7) spruce-conifer-broadleaf mixed forests. The collected data included the amount of *I. typographus* damage and the location and composition of the infested forests. The results indicate that different forest types are differently susceptible to *I. typographus*. Plantations, reforestations and mountain spruce forests show mean damage and mean number of infestations higher than other forest types. Within pure spruce forests, alpine forests growing at high elevations (>1300 m) suffer low damage. Furthermore, the mean number of infestation spots recorded annually in the different spruce forest types is negatively correlated with a Naturality Index value. The results suggest that forest composition and elevation are the main factors driving the risk of *I. typographus* damage. A new management strategy for some spruce forest types is needed, with a progressive reduction of pure spruce forests at low altitude and an increase of broadleaf composition.

Keywords: Scolytinae; *Ips typographus*; forest management; outbreaks; Southern Alps; Italy

1. Introduction

Forest composition and temperature are among the main environmental factors affecting tree suitability to herbivorous insects and, hence, management decisions concerning the control of forest pests [1]. Knowledge on the spatio-temporal distribution and population density of the major forest pests should be the first step towards an integrated forest management focused on forest protection and timber production. According to the theory of predisposition and trigger [2], insect outbreaks rely on a spatial and temporal coincidence of susceptible (*i.e.*, predisposed) forests with disturbance factors affecting tree survival and the production of ecosystem goods and services [3]. Although foresters cannot determine the occurrence of unpredictable disturbance factors, they can affect the forest health by accurate silvicultural planning and management [4]. The poor health conditions of forests growing in sites characterized by environmental traits unsuitable for a particular tree species, such as frequent climatic anomalies, elevation, soil characteristics and forest composition, are expected to trigger insect infestations, with potentially serious consequences on forest survival [5,6].

Bark beetles (Coleoptera: Curculionidae, Scolytinae) are probably the most important pests affecting Holarctic forests [7,8]. Many studies on the population dynamics of bark beetles suggest that climatic anomalies, such as drought and heat waves, may trigger large insect outbreaks [8–10], acting both directly on the insect populations and indirectly on the health of the potential host trees. In the last few years, the spruce bark beetle, *Ips typographus* (L.), one of the most destructive insects infesting spruce forests (*Picea abies* Karsten), caused serious damage almost everywhere in Europe [3,11–13]. Severe damage was also recorded in spruce forests growing on the Southern Alps [14–19]. Large *I. typographus* outbreaks were observed mainly in sites with environmental conditions not fully suitable for spruce. Recent studies carried out on the south-eastern Alps show, for instance, a mean damage per hectare about seven times higher in spruce forests growing in sites warmer than those within the natural climatic range of spruce [19]. Moreover, the intensity and altitudinal distribution of the insect outbreaks were affected by dry summers, which were related to an increase of the mean damage [17] and an upward shift of the altitudinal outbreak range [19]. A preliminary investigation carried out in the same region reported that silvicultural practices may substantially modify the susceptibility of spruce trees to *I. typographus* infestations [20]. Damage caused by *I. typographus* was recorded in different types of spruce forests, showing a strong variation among the monitored forest types. However, the recorded variables were just some of the main parameters that could determine the availability of weakened or dying host trees and, hence, the type of spruce forests [20]; so, a more detailed analysis is required.

Better knowledge of the relationships between forest composition and pest outbreaks could help foresters in applying silvicultural practices suitable for minimizing the present and future damage due to forest pests. Decision-making in forest pest management calls for tools that can help in understanding the relationships among predisposing factors, forest characteristics and pest

occurrence [4], improving the pest control strategies and reducing general costs. In this study, we hypothesize that forest composition, together with climatic conditions, may affect *I. typographus*-induced damage, and we assume that the damage is lower in high-diversity Norway spruce forests and in stands growing at higher elevations, which is considered a proxy for temperature. The aim of the paper is, therefore, to investigate the differences in the severity of the spruce bark beetle attacks among seven types of spruce forests growing on the Southern Alps and differing mainly in tree species composition, tree origin (*i.e.*, from natural seedlings or planted) and elevation.

2. Experimental Section

2.1. Study Species

The spruce bark beetle, *I. typographus*, is one of the main European forest pests [21,22]. The species causes great damage also to spruce stands growing along the Southern Alps [11,14–16,18]. Adults of the parental generation leave the overwintering sites in spring (May), when the mean air temperature is about 18 °C [23], and fly looking for suitable hosts, *i.e.*, stressed or dying spruces, where they begin the first generation. In general, *I. typographus* populations living along the Southern Alps are bivoltine [14–16,18]. At the beginning of July, the offspring emerges and starts a second generation, which will end in September. After overwintering under the bark or in the litter [24], the offspring of the second generation will emerge in the spring of the following year.

Ips typographus usually infests stressed or dying trees and can respond quickly to the abundance of suitable hosts induced by weather events and unfavorable stand conditions [11]. During infestations, *I. typographus* has a natural tendency to aggregate and produce easily recognizable clusters of infested trees (hereafter called “spots”). In the following years, spots enlarge, partially affecting trees that have recovered from stress, also. The outbreak dynamics are often driven by negative feedback mechanisms, such as intraspecific competition [11]. As *I. typographus* kills trees to reproduce, tree mortality is positively related to population abundance [14,25].

2.2. Study Area and Naturality Index

The study was conducted in the Friuli Venezia Giulia region (NE Italy), a mountainous area of 7844 km² located along the southern border of the Alps (Figure 1). Norway spruce is the main forest species in this area, covering about 66,100 ha scattered in 7 main types of mixed and pure forests (Table 1), where spruce is usually growing along the southern edge of its climatic range, as defined by Schmidt-Vogt [26]. Del Favero *et al.* [27,28] calculated a Naturality Index for each of the 7 types of spruce forests. The Naturality Index, calculated following the protocol proposed by Poldini [29] and Poldini and Pertot [30], assesses the natural origin of the forest in relation to the occurrence of human modifications [31,32]. In a scale of 1–5, the Naturality Index indicates a status close to (high values) or far from (low values) the natural origin of the forests. Del Favero *et al.* [27,28] inspected all stands belonging to a specific forest type, assigning a Naturality Index to each stand; all values were then averaged, giving the mean Naturality Index of each forest type [27,28].

2.3. Spruce Forest Types

According to the Habitat Classification of the European Nature Information System (EUNIS) [33] and Del Favero *et al.* [27,28], spruce forests in the Friuli Venezia Giulia region can be classified as follows:

Figure 1. Italian region where the study was carried out. For the legend of the forest type codes, see Table 1.

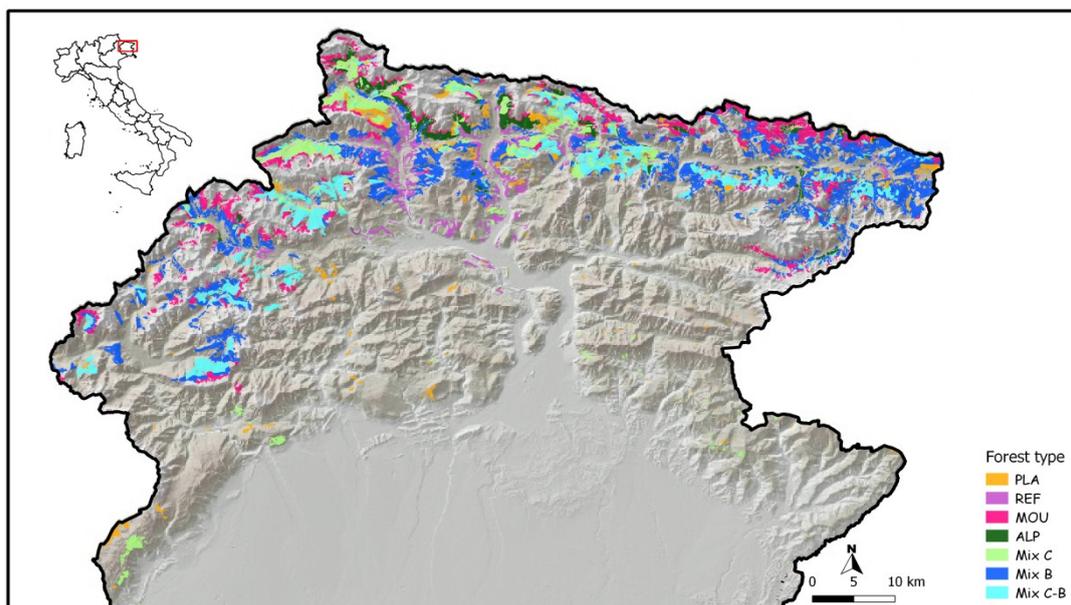


Table 1. Main types of spruce forests occurring in the investigated area and their characteristics. The values of dendrometric parameters are reported as mean \pm standard deviation.

Spruce forest types	Code	Area (ha)	Area (%)	Elevation (m a.s.l.)	DBH ¹ (cm)	Density ² (trees per ha)	Naturality Index ³
Pure spruce plantations	PLA	4514	6.8	718 \pm 147	31.4 \pm 0.5	358 \pm 17	1.0
Pure spruce reforestations	REF	4844	7.3	940 \pm 299	35.5 \pm 0.8	325 \pm 8	1.3
Pure spruce mountain forests	MOU	3729	5.6	1022 \pm 298	33.1 \pm 0.3	265 \pm 6	2.5
Pure spruce alpine forests	ALP	10,429	15.7	1502 \pm 174	35.1 \pm 0.4	250 \pm 11	4.0
Spruce-conifer mixed forests	Mix C	7512	11.3	989 \pm 282	34.1 \pm 0.4	298 \pm 7	3.0
Spruce-broadleaf mixed forests	Mix B	24,203	36.6	1175 \pm 216	31.7 \pm 0.4	278 \pm 4	3.8
Spruce-conifer-broadleaf mixed forests	Mix C-B	10,846	16.4	1184 \pm 174	31.5 \pm 0.5	288 \pm 9	4.0
Total	–	66,080	100	–	–	–	–

¹ The values of the diameter at breast height (DBH) refer only to the spruce trees occurring in each investigated area; ² the values of tree density refer to all trees species (spruce, conifers and broadleaves) occurring in each investigated area; ³ the Naturality Index is as reported by Del Favero *et al.* [27,28] and calculated as in Poldini [29] and Poldini and Pertot [30].

(1) Pure spruce plantations (PLA): non-native pure and even-aged spruce plantations normally growing in small stands at low elevation (about 700 m a.s.l.; range 550–850) and characterized by a generally warm climate. Unlike all other spruce formations, plantations are usually located outside the

natural climatic range of spruce [26]. In these habitats, spruce often replaces native forests of broadleaves after their felling. They are stands with high tree density (about 350 trees per ha) and without brushwood. This spruce formation covers about 4500 ha, representing *ca.* 6.8% of the spruce forests of the investigated area. They are man-made forests with a very low value (1.0) of the Naturality Index [27,28] (Table 1).

(2) Pure spruce reforestations (REF): natural pure spruce forests growing at about 900 m a.s.l. (range 650–1200), where they replace mixed broadleaf forests or grasslands and meadows. These formations result from past silvicultural practices supporting the spread of spruce by the periodic elimination of native oak, chestnut and beech forests. They cover about 4800 ha, representing *ca.* 7.3% of the total spruce forests of the region; a Naturality Index of 1.3 (Table 1).

(3) Pure spruce mountain forests (MOU): pure and even-aged spruce forests growing on fertile acidophil soils. Natural formations usually growing along steep slopes at about 1000 m a.s.l. (range 700–1300 m), with high tree density and scarce brushwood. Covering only about 3700 ha, MOU are the rarest spruce formations in Friuli Venezia Giulia (less than 6%); a Naturality Index of 2.5 (Table 1).

(4) Pure spruce alpine forests (ALP): natural high-elevation pure spruce forests growing in the most northern areas at about 1500 m a.s.l. (range 1350–1700), where temperatures are generally cold. Here, spruce grows in its best conditions [26]. This type of spruce formation covers about 10,500 ha, representing *ca.* 15.7% of all the spruce forests in the region. The low tree density (about 250 trees per ha) and rich brushwood result in a high (4.0) Naturality Index (Table 1).

(5) Spruce-conifer mixed forests (Mix C): natural conifer mixed forests, where spruce grows with either larch, fir or Scots pine, according to local climate and soil conditions. These formations occur at about 1000 m a.s.l. (range 700–1200), with the dominance of different conifer species depending on the habitat conditions and previous forest management. They cover about 7500 ha, representing *ca.* 11.3% of the spruce forests. Large and old trees are common; a Naturality Index of 3.0 (Table 1).

(6) Spruce-broadleaf mixed forests (Mix B): natural spruce formations mixed with broadleaves, usually beech, mostly growing at about 1200 m a.s.l. (range 950–1400) along south-facing slopes, where climatic conditions are favorable to both of the species. The proportion of spruce and broadleaves is affected by past silvicultural practices, local soil conditions and air humidity. They are usually growing on carbonate soils with high water availability, due to frequent rainfall. The natural association between spruce and beech is the most common forest type in the region, covering a surface of about 24,200 ha, *i.e.*, more than a third (36.6%) of the spruce forests; a Naturality Index of 3.8 (Table 1).

(7) Spruce-conifer-broadleaf mixed forests (Mix C-B): natural uneven-aged spruce forests mixed with fir and beech. These are forests growing at about 1200 m a.s.l. (range 1000–1350) on deep and fertile soils, with the proportion of spruce, fir and beech, depending on the local microclimate and silvicultural conditions. This forest type usually grows in sites having silicate soils with reduced water availability and managed with limited silvicultural pressure. They are the second widest spruce formations in Friuli Venezia Giulia, involving about 10,800 ha and representing *ca.* 16.4% of the spruce forests. The occurrence of many tree species in the same site results in a high (4.0) Naturality Index (Table 1).

The mean rainfall regime is similar in all forest types, with about 1200 mm per year.

2.4. Data Collection

Data on *I. typographus* infestations were obtained from the phytopathologic forest inventory of the Friuli Venezia Giulia region (BAUSINVE) [34]. Since 1994 BAUSINVE provides information about forest pests and diseases occurring in the regional forests [35]. Forest health of the whole region is monitored daily via ground-based survey by about 60 foresters working for the Regional Forest Service and supervised by a team of entomologists and pathologists from scientific institutes. When an outbreak occurs, foresters compile specific reports, including information concerning both the infesting pest (species, development instar, population density) and the total damage (number of trees attacked, volume of infested timber, defoliation area). During the survey, the foresters also classify the characteristics of the attacked forests, collecting data on elevation, tree density, composition, structure, type of forest and management. Data are then recorded and stored in an electronic database. Our database thus derives from a long-term intensive forest health monitoring covering a 19-year period (1994–2012). Each recorded infestation spot composed of at least 5 infested trees was visited to identify the biotic agent causing tree mortality, recording the number of killed trees, the volume of timber loss (m^3) and the site characteristics. Using these data, we built a time series of annual timber loss for the whole region by summing the volume (m^3) of trees killed in all the spots occurring each year in each forest type. Annual timber loss also included spots detected in the spring of the following year to allow for the delay between late-summer beetle infestations by second or even third generations [18] and canopy discoloration occurring in the next spring.

2.5. Statistical Analysis

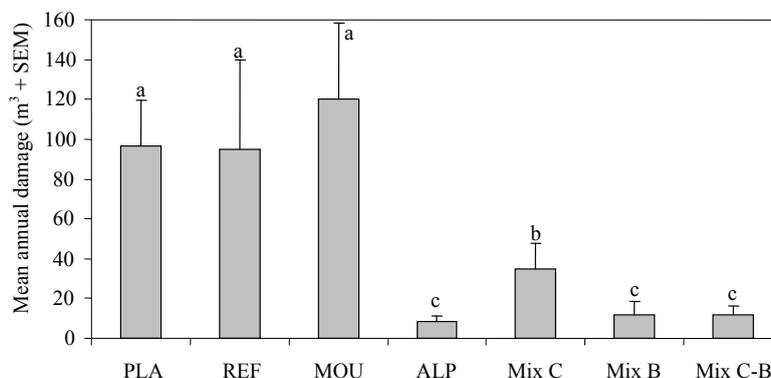
We tested the hypothesis that all spruce forest types were equally susceptible to *I. typographus* infestations, by comparing the mean damage (m^3) recorded in the last 19 years in the monitored spruce forests. The mean annual volume of timber infested by *I. typographus* was used as the main dependent variable, because this was carefully measured and is of high practical utility for foresters, but also because it is a reasonable proxy for beetle abundance and, therefore, allows for qualified inferences regarding population dynamics. However, because the compared spruce forest types have different extensions (Table 1), the mean annual volume recorded for each spruce forest type was reported to be a standard area of 1000 ha ($\text{m}^3/1000$ ha). Because the susceptibility of a forest to a pest may also be assessed considering the temporal infestation frequency and the size of each single infestation event, the different spruce forest types were also compared for the mean number and size of the spots recorded during the 19-year survey. Analysis of variance (ANOVA) was used to find significant differences among spruce forest types in terms of mean annual damage, mean annual number of spots and mean spot size [36]. The homogeneity of variance was tested by Cochran's test (test C) and normality by the Kolmogorov–Smirnov test (test D). When necessary, data were log- [$X' = \log(x + 1)$] or arcsin- ($X' = \arcsin\sqrt{x}$) transformed to obtain the homogeneity of the variance and normality. Wherever significant differences occurred, Tukey's honestly significant difference (HSD) multiple comparison test was applied for mean separation [36]. The mean number of spots reported every 1000 ha was lastly correlated by a linear regression model with the degree of naturalness of the monitored types of spruce forests. An R^2 value, adjusted for the number of parameters [36], was used

to assess the goodness-of-fit of the tested model. Differences at the 0.05 confidence level were considered significant. Analyses were performed by Statistica for Windows (Statistica, Tulsa, OK, USA).

3. Results

In the 19-year monitoring, 797 infestation spots of *I. typographus* were recorded, for a total of 30,475 infested spruce trees (1604 per year) and about 37,780 m³ (1988 per year) of damaged timber. As hypothesized, different forest types were differently susceptible to *I. typographus* infestations, suffering damage of different intensity (ANOVA, $df = 6$; 119, $F = 3.84$, $p < 0.001$). In particular, PLA, REF and MOU showed a mean damage significantly higher than the other forest types (Tukey test, $p < 0.05$), with values close to or greater than 100 m³ of timber lost annually per 1000 ha (Figure 2). Instead, ALP, Mix B and Mix C-B were less prone to *I. typographus* infestations, with a mean damage about 10 times lower than the previous types. Finally, Mix C had damage of about 35 m³ of timber per year every 1000 ha of forest (Figure 2).

Figure 2. Mean annual damage recorded in different forest types (m³ every 1000 ha). Different letters indicate significant differences at $p < 0.05$. For the code legend, see Table 1.



The mean annual number of infestation spots recorded every 1000 ha also significantly differed among forest types (ANOVA, $df = 6$; 119, $F = 4.30$, $p < 0.001$) (Figure 3), showing a very similar trend to those reported for annual damage. PLA, REF and MOU had a mean number of infestation spots higher than other forest types (Tukey test, $p < 0.05$), with values close to or more than 10 spots per year every 1000 ha (Figure 3). Instead, ALP, Mix B and Mix C-B suffered the lowest numbers of infestations. Again, Mix C showed a value in between (Figure 3). Interestingly, the size of the infestation spots was similar in all forest types (ANOVA, $df = 6$; 794, $F = 0.57$, $p = 0.75$), with a mean value of about 40 m³ per spot (Figure 4).

Figure 3. Mean annual number of infestation spots recorded in different forest types every 1000 ha of spruce forest. Different letters indicate significant differences at $p < 0.05$. For the code legend, see Table 1.

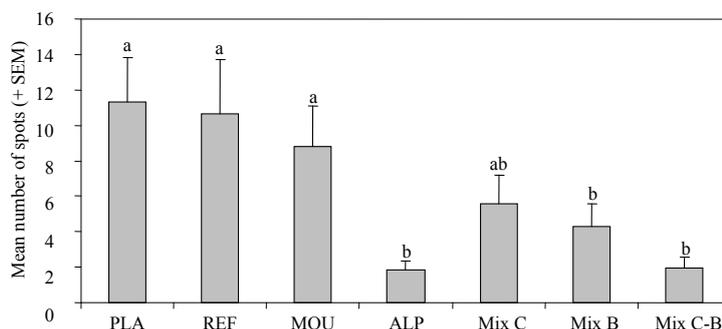
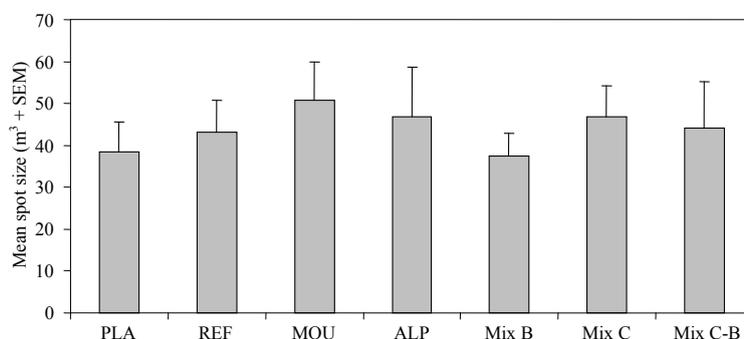


Figure 4. Mean size (m^3) of the infestation spots recorded in different spruce forest types. For the code legend, see Table 1.

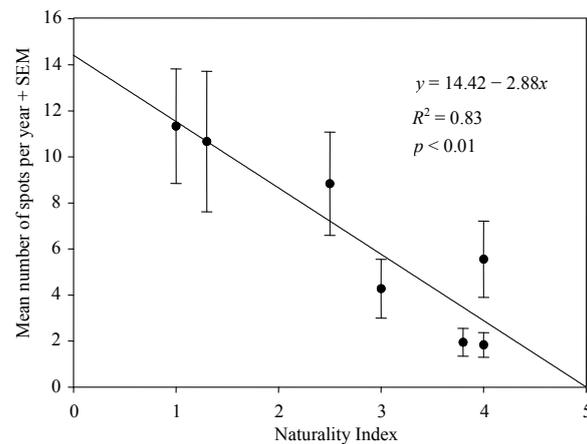


The mean number of infestation spots recorded annually in the different spruce forest types was negatively correlated with the Naturalness Index of the monitored forests ($F = 25.56$; $R^2 = 0.83$; $p < 0.01$) (Figure 5), with spruce forests intensively managed, such as PLA and REF (Table 1), suffering the highest number of *I. typographus* spots.

4. Discussion

We found that different forest types suffer damage of different severity. Spruce forests, usually characterized by low diversity (a Naturalness Index equal to or lower than 2.5), such as plantations, reforestation and mountain forests, show the highest mean damage per year. In other forest types, *I. typographus* damage is instead mitigated by either the high diversity of the spruce mixed forests or the high elevation of the alpine forests. Damage caused by *I. typographus* was hence driven mainly by forest diversity, *i.e.*, forest composition, and elevation, which directly affect tree resistance to insect colonization and indirectly affect insect population dynamics regulating the availability of susceptible host material.

Figure 5. Correlation between the Naturality Index of different spruce forest types and the mean number of infestation spots suffered annually.



Results from this study clearly show that in forests growing at similar elevations, *I. typographus* infestations were largely influenced by forest composition, with mixed forests being less susceptible to bark beetle damage than pure spruce forests. This may be the result of several factors, which, however, often concern the physiological conditions and defenses of the potential host tree. Preformed or constitutional resin released upon attempted penetrations of the bark is, for instance, one of the main spruce defense mechanisms against *I. typographus* [37]. In this respect, trees growing in mixed stands have been reported to have a higher resin flow than spruces from pure stands, increasing tree defense reactions against bark beetles and their associated fungi [38]. Multi-tree species forests may also affect bark beetle chemical communication. Non-host volatiles, and, particularly, green leaf volatiles, released by broadleaves are known to reduce both *I. typographus* breeding performance [39] and its ability to find suitable host trees in mixed forests [40,41]. Similar results were found by Hlásny and Turčáni [3] in Central Europe. These authors suggest that the large infestations recorded in many European countries in the last few decades can be explained by the species composition of the monitored forests. Tree species composition is also an important predictor in bark beetle hazard rating models, such as Predisposition Assessment Systems [4]. In this respect, an ecologically sustainable strategy to reduce the risk of *I. typographus* damage, especially in managed spruce forests, should be focused on forming stands with heterogeneous composition, reducing the proportion of spruce [11]. A low amount of suitable breeding material, *i.e.*, spruce, may prevent pests from building up their populations [42], whereas non-host trees may provide physical and chemical barriers to host location or colonization. Accordingly, our results show a mean number of infestation spots per year negatively correlated with the Naturality Index of the monitored forest types, with damage higher in pure (low index) than in mixed (high index) spruce forests.

Not just forest composition may affect the intensity of *I. typographus* damage. Within pure spruce forests, different forest types differently suffer *I. typographus* infestations, with spruce alpine forests growing at a high elevation (1300–1700 m a.s.l.) showing the lowest damage. A recent study by Chinellato *et al.* [43] explores how elevation, as a proxy for temperature, affects the abundance and

diversity of bark and wood boring beetles associated with Norway spruce along the southern edge of the Alps. The paper shows that aggressive bark beetle species, such as *I. typographus*, respond positively to higher temperature, infesting spruce forests located at low elevations, *i.e.*, warmer, more intensively than alpine forests [43]. Growing in sites frequently exposed to unfavorable climatic conditions may reduce tree defenses against both climate disturbances and insect colonization [44]. Recent studies from northern [13] and central Europe [3] report that the availability of breeding substrates and the ability of *I. typographus* to colonize spruce trees growing in suboptimal conditions are the main abiotic factors triggering *I. typographus* outbreaks. A number of environmental factors may indirectly affect the population dynamics of *I. typographus*, acting on the susceptibility of the host trees through severe climate events, e.g., drought, heat waves, wind or snow storms, occurring in sites unsuitable for spruce growing [11,17,19]. In this respect, the warm summer temperature recorded in the last few years in southern Europe [45] became one of the main factors affecting the general health conditions of spruce forests [46]. Long, warm and dry summers may enhance tree susceptibility to forest pests [11,17,19], and *I. typographus* outbreaks were often associated with these events [11]. In the same region where this study was carried out, Marini *et al.* [19] found an altitudinal distribution of *I. typographus* damage correlated with summer temperature and insect outbreak dynamics. Warm temperatures occurring at low elevations make spruce forests particularly vulnerable to *I. typographus* outbreaks [3,19]. The same mechanism was observed worldwide also in other conifer bark beetles [8]. Warm temperatures occurring at low elevations affect *I. typographus* also directly. In general, *I. typographus* populations living along the Southern Alps are bivoltine at a low altitude (<1300–1400 m a.s.l.) [15,18]. Warm temperatures and long summers occurring at low altitudes allow high rates of development, with an increase in the number of generations per year, as suggested by several prediction models [47–50]. Eruptions of bark beetle populations have often been associated with change in voltinism. Increased outbreaks of the spruce beetle, *Dendroctonus rufipennis* (Kirby), recorded in Alaska in the 1990s [51] have been, for instance, associated with a shift from a two-year to a one-year developmental cycle [52,53]. Faccoli and Bernardinelli [18] recently investigated the breeding performance of the second generation in some bivoltine populations of *I. typographus* in the south-eastern Alps, suggesting that climate factors deeply influence the number of suitable hosts available to the second generation and, hence, the population growth. In conclusion, pure spruce forests growing at low elevations (<1300 m) suffer high bark beetle damage, because of warm temperatures stressing the trees, reducing host resistance to insect colonization, and allowing for a full second generation of the *I. typographus* populations.

Finally, our results show that all considered forest types have infested trees, *i.e.*, spruce diameter, and infestation spots with a similar mean size, suggesting that the total damage suffered by different spruce forest types is affected mainly by the number and frequency of the infestation spots rather than their size. In other words, once an *I. typographus* infestation begins, usually triggered by climatic events stressing spruce, its natural development proceeds independently from the forest composition and may terminate several years later following negative feedback mechanisms, such as intraspecific competition and natural enemies [11,21]. In this respect, the probability of new infestations becomes the crucial point to assess the forest's risk of suffering *I. typographus* damage. A similar mechanism was reported for populations of the pine engraver beetle, *Ips acuminatus* (Gyllenhal), occurring in the

south-eastern Alps [54], where, in years of high population density following drought periods, the number of infestation spots, but not their size, was significantly higher than in years of low density.

5. Conclusions

The recent intensification of bark beetle outbreaks recorded in European spruce forests [55] calls for a new management strategy, with a progressive reduction of pure spruce forests, especially at low elevations, and an increase in their ecological stability [3]. Spruce should be mixed with tree species better adapted to the specific site characteristics and the new climatic conditions expected for the future [56]. Increasing forest diversity by the introduction of broadleaf species will improve resistance to bark beetle infestations [57] and will assure the production of sustainable ecosystem goods and services [3]. Forest protection measures should therefore be allocated according to the rating of the stand hazard based on site and stand characteristics, which vary among forest types. Within the perspective of a general improvement of tree health conditions, forest management should, moreover, shift from the stand to the regional scale, progressively reducing pure spruce forests or improving their general growing conditions. In conclusion, considering the potential increased susceptibility of spruce forests to *I. typographus* outbreaks due to climate change, there is increasing value in mitigating these effects through sustainable forest management, which includes the reduction of pure and intensive spruce cultivations and the improvement of their growing conditions [19].

Acknowledgments

The authors thank two anonymous reviewers for constructive comments on earlier versions of the manuscript and Alison Garside for linguistic proofreading. Research carried out within the project “BAUSINVE” (Direzione Centrale attività produttive, commercio, cooperazione, risorse agricole e forestali); ERSA, agenzia regionale per lo sviluppo agricolo, Regione Autonoma Friuli Venezia Giulia (Italy).

Conflicts of Interest

The authors declare no conflict of interest.

References

1. Speight, M.R.; Wainhouse, D. *Ecology and Management of Forest Insects*; Clarendon Press: Oxford, UK, 1989; p. 374.
2. Manion, P.D. *Tree Disease Concepts*, 2nd ed.; Prentice Hall: Englewood Cliffs, NJ, USA, 1991; p. 402.
3. Hlásny, T.; Turčáni, M. Persisting bark beetle outbreak indicates the unsustainability of secondary Norway spruce forests: Case study from Central Europe. *Ann. For. Sci.* **2013**, *70*, 481–491.
4. Netherer, S.; Nopp-Mayr, U. Predisposition Assessment Systems (PAS) as supportive tools in forest management: Rating of site and stand-related hazards of bark beetle infestation in the High Tatra Mountains as an example for system application and verification. *For. Ecol. Manag.* **2005**, *207*, 99–107.

5. Jönsson, A.M.; Schroeder, L.M.; Lagergren, F.; Anderbrant, O.; Smith, B. Guess the impact of *Ips typographus*—An ecosystem modelling approach for simulating spruce bark beetle outbreaks. *Agric. For. Meteorol.* **2012**, *166–167*, 188–200.
6. Overbeck, M.; Schmidt, M. Modelling infestation risk of Norway spruce by *Ips typographus* (L.) in the Lower Saxon Harz Mountains (Germany). *For. Ecol. Manag.* **2012**, *266*, 115–125.
7. Lieutier, F.; Day, K.R.; Battisti, A.; Grégoire, J.-C.; Evans, H.F. *Bark and Wood Boring Insects in Living Trees in Europe, A Synthesis*; Kluwer Academic Publishers: Dordrecht, UK, 2004; p. 569.
8. Raffa, K.F.; Aukema, B.H.; Bentz, B.J.; Carroll, A.L.; Hicke, J.A.; Turner, M.G.; Romme, W.H. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: Dynamics of biome-wide bark beetle eruptions. *BioScience* **2008**, *58*, 501–517.
9. Allen, C.D.; Macalady, A.K.; Chenchouni, H.; Bachelet, D.; McDowell, N.; Vennetier, M.; Kitzberger, T.; Rigling, A.; Breshears, D.D.; Hogg, E.H.; *et al.* A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manag.* **2010**, *259*, 660–684.
10. Jactel, H.; Petit, J.; Desprez-Loustau, M.-L.; Delzon, S.; Piou, D.; Battisti, A.; Koricheva, J. Drought effects on damage by forest insects and pathogens: A meta-analysis. *Glob. Chang. Biol.* **2012**, *18*, 267–276.
11. Wermelinger, B. Ecology and management of the spruce bark beetle, *Ips typographus*—A review of recent research. *For. Ecol. Manag.* **2004**, *202*, 67–82.
12. Jönsson, A.M.; Harding, S.; Krokene, P.; Lange, H.; Lindelöw, Å.; Økland, B.; Ravn, H.P.; Schroeder, L.M. Modelling the potential impact of global warming on *Ips typographus* voltinism and reproductive diapause. *Clim. Chang.* **2011**, *109*, 695–718.
13. Marini, L.; Lindelöw, A.; Jönsson, A.M.; Wulff, S.; Schroeder, L.M. Population dynamics of the spruce bark beetle: A long-term study. *Oikos* **2013**, *122*, 1768–1776.
14. Faccoli, M.; Stergulc, F. *Ips typographus* (L.) pheromone trapping in south Alps: Spring catches determine damage thresholds. *J. Appl. Entomol.* **2004**, *128*, 307–311.
15. Faccoli, M.; Stergulc, F. A practical method for predicting the short-time trend of bivoltine populations of *Ips typographus* (L.) (Col., Scolytidae). *J. Appl. Entomol.* **2006**, *130*, 61–66.
16. Faccoli, M.; Stergulc, F. Damage reduction and performance of mass trapping devices for forest protection against the spruce bark beetle, *Ips typographus* (Coleoptera Curculionidae Scolytinae). *Ann. For. Sci.* **2008**, *65*, 309.
17. Faccoli, M. Effect of weather on *Ips typographus* (Coleoptera Curculionidae) phenology, voltinism and associated spruce mortality in the south-eastern Alps. *Environ. Entomol.* **2009**, *38*, 307–316.
18. Faccoli, M.; Bernardinelli, I. Breeding performance of the second generation in some bivoltine populations of *Ips typographus* (Coleoptera Curculionidae) in the south-eastern Alps. *J. Pest Sci.* **2011**, *84*, 15–23.
19. Marini, L.; Ayres, M.P.; Battisti, A.; Faccoli, M. Climate affects severity and altitudinal distribution of outbreaks in an eruptive bark beetle. *Clim. Chang.* **2012**, *115*, 327–341.
20. Bernardinelli, I.; Stergulc, F.; Frigimelica, G.; Zandigiacomo, P.; Faccoli, M. Spatial analysis of *Ips typographus* infestations in South-Eastern Alps. In Proceedings of the Workshop on Methodology of Forest Insect and Disease Survey in Central Europe (IUFRO Working Party

- 7.03.10), Forest Training Centre, Gmunden, Austria, 11–14 September 2006; Forster, B., Knížek, M., Grodzki, W., Eds.; Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW): Gmunden, Austria, 2008; pp. 45–52.
21. Christiansen, E.; Bakke, A. The Spruce Bark Beetle of Eurasia. In *Dynamics of Forest Insect Populations*; Berryman, A.A., Ed.; Plenum Publishing Corporation: New York, USA, 1988; pp. 479–503.
 22. Grégoire, J.-C.; Evans, H.F. Damage and Control of BAWBILT Organisms, an Overview. In *Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis*; Lieutier, F., Day, K.R., Battisti, A., Grégoire, J.-C., Evans, H.F., Eds.; Kluwer Academic Publishers: London, UK, 2004; pp. 19–37.
 23. Annala, E. Influence of the temperature upon the development and voltinism of *Ips typographus* L. (Coleoptera, Scolytidae). *Ann. Zool. Fenn.* **1969**, *6*, 161–207.
 24. Faccoli, M. Winter mortality in sub-corticolous populations of *Ips typographus* (Coleoptera Scolytidae) and its parasitoids in the South-eastern Alps. *J. Pest Sci.* **2002**, *75*, 62–68.
 25. Franklin, A.; de Canniere, C.; Grégoire, J.-C. Can sales of infested timber be used to quantify attacks by *Ips typographus* (Coleoptera, Scolytidae)? A pilot study from Belgium. *Ann. For. Sci.* **2004**, *61*, 477–480.
 26. Schmidt-Vogt, H. *Die Fichte Band I. Taxonomie-Verbreitung-Morphologie-Ökologie-Waldgesellschaften*; Verlag Paul Parey: Hamburg and Berlin, Germany, 1977; p. 647.
 27. Del Favero, R.; Poldini, L.; Bortoli, P.L.; Dreossi, G.; Lasen, C.; Vanone, G. *La Vegetazione Forestale e la Selvicoltura Nella Regione Friuli Venezia Giulia*; Regione Autonoma del Friuli Venezia Giulia, Direzione Regionale Foreste, Servizio Selvicoltura: Trieste, Italy, 1998; Volume 1, p. 490.
 28. Del Favero, R.; Poldini, L.; Bortoli, P.L.; Dreossi, G.; Lasen, C.; Vanone, G. *La Vegetazione Forestale e la Selvicoltura Nella Regione Friuli Venezia Giulia*; Regione Autonoma del Friuli Venezia Giulia, Direzione Regionale Foreste, Servizio Selvicoltura: Trieste, Italy, 1998; Volume 2, p. 303.
 29. Poldini, L. *La Vegetazione del Carso Isontino e Triestino*; LINT Edizioni: Trieste, Italy, 1989; p. 315.
 30. Poldini, L.; Pertot, M. Criteri di indicizzazione del valore naturalistico sull'esempio del Carso triestino-goriziano. *Soc. Bot. Ital.* **1989**, *21*, 133–151.
 31. von Hornstein, F. *Wald und Mensch*; O. Maier Verlag: Ravensburg, Germany, 1951.
 32. Remmert, H. *Ökologie*; Springer: Berlin, Heidelberg, Germany, New York, NY, USA, 1976.
 33. European Nature Information System, EUNIS. Available online: <http://eunis.eea.europa.eu/habitats.jsp> (accessed on 09 January 2014).
 34. BAUSINVE, Regione Autonoma Friuli Venezia Giulia. Available online: <http://www.regione.fvg.it/rafvfg/cms/RAFVG/economia-impres/agricoltura-foreste/foreste/FOGLIA4/> (accessed on 09 January 2014).
 35. Stergulc, F.; Frigimelica, G.; Carpanelli, A. L'inventario Fitopatologico Forestale del Friuli-Venezia Giulia: Metodologie e Risultati di un Programma di Monitoraggio Permanente dello Stato Fitosanitario delle Foreste. In *Proceedings of the Monitoraggio dello Stato Fitosanitario delle Foreste: Esperienze a Confronto*, Florence, Italy, 12 Aprile 2002; Arsia Toscana Ed.; pp. 83–92.
 36. Zar, J.H. *Biostatistical Analysis*; Prentice Hall Press: Upper Saddle River, NJ, USA, 1999; p. 898.

37. Paine, T.D.; Raffa, K.F.; Harrington, T.C. Interactions among scolytid bark beetles, their associated fungi, and live host conifers. *Annu. Rev. Entomol.* **1997**, *42*, 179–206.
38. Baier, P.; Führer, E.; Kirisits, T.; Rosner, S. Defence reactions of Norway spruce against bark beetles and the associated fungus *Ceratocystis polonica* in secondary pure and mixed species stands. *For. Ecol. Manag.* **2002**, *159*, 73–86.
39. Faccoli, M.; Blaženec, M.; Schlyter, F. Feeding response to host and non-host compounds by males and females of the spruce bark beetle *Ips typographus* in a tunnelling microassay. *J. Chem. Ecol.* **2005**, *31*, 745–759.
40. Byers, J.A.; Zhang, Q.H.; Schlyter, F.; Birgersson, G. Volatiles from nonhost birch trees inhibit pheromone response in spruce bark beetles. *Naturwiss* **1998**, *85*, 557–561.
41. Zhang, Q.H.; Schlyter, F.; Anderson, P. Green leaf volatiles interrupt pheromone response of spruce bark beetle *Ips typographus*. *J. Chem. Ecol.* **1999**, *25*, 2847–2861.
42. Jactel, H.; Brockerhoff, E. Tree diversity reduces herbivory by forest insects. *Ecol. Lett.* **2007**, *10*, 835–848.
43. Chinellato, F.; Faccoli, M.; Marini, L.; Battisti, A. Distribution of Norway spruce bark and wood boring beetles along Alpine elevational gradients. *Agric. For. Entomol.* **2013**, doi:10.1111/afe.12040.
44. Økland, B.; Berryman, A. Resource dynamics plays a key role in regional fluctuations of the spruce bark beetle *Ips typographus*. *Agric. For. Entomol.* **2004**, *6*, 141–146.
45. IPCC. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment. In *Report of the Intergovernmental Panel on Climate Change*; Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L., Eds.; Cambridge University Press: Cambridge, UK, New York, NY, USA, 2007, p. 996.
46. Schelhaas, M.-J.; Nabuurs, G.-J.; Schuck, A. Natural disturbances in the European forests in the 19th and 20th centuries. *Glob. Chang. Biol.* **2003**, *9*, 1620–1633.
47. Lange, H.; Økland, B.; Krokene, P. Thresholds in the life cycle of the spruce bark beetle under climate change. *Inter. J. Complex. Syst.* **2006**, *1648*, 1–10.
48. Baier, P.; Pennerstorfer, J.; Schopf, A. PHENIPS—A comprehensive phenology model of *Ips typographus* (L.) (Col., Scolytinae) as a tool for hazard rating of bark beetle infestation. *For. Ecol. Manag.* **2007**, *249*, 171–186.
49. Jönsson, A.M.; Harding, S.; Barring, L.; Ravn, H.P. Impact of climate change on the population dynamics of *Ips typographus* in southern Sweden. *Agr. For. Meteorol.* **2007**, *146*, 70–81.
50. Jönsson, A.M.; Appelberg, G.; Harding, S.; Barring, L. Spatiotemporal impact of climate change on the activity and voltinism of the spruce bark beetle, *Ips typographus*. *Glob. Chang. Biol.* **2009**, *15*, 486–499.
51. Wittwer, D.; Matthews, K.; Zogas, K.; Trummer, L.; Holsten, E.; Schulz, B.; Hennon, P.; Schultz, M.; Riggs, J.; Burnside, R. Forest Insect and Disease Conditions in Alaska, 1998; General Technical Report US Forest Service R10-TP-74; USDA Forest Service, Forest Health Protection-Alaska Region: Anchorage, AK, USA, November, 1988.
52. Hansen, E.M.; Bentz, B.J. Comparison of reproductive capacity among univoltine, semivoltine, and re-emerged parent spruce beetles (Coleoptera: Scolytidae). *Can. Entomol.* **2003**, *135*, 697–712.

53. Berg, E.E.; Henry, J.D.; Fastie, C.L.; DeVolder, A.D.; Matsuoka, S.M. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. *For. Ecol. Manag.* **2006**, *227*, 219–232.
54. Colombari, F.; Schroeder, M.L.; Battisti, A.; Faccoli, M. Spatio-temporal dynamics of an *Ips acuminatus* outbreak and implications for management. *Agric. For. Entomol.* **2013**, *15*, 34–42.
55. Uniyal, S.K.; Uniyal, A. Climate change and large-scale degradation of spruce: Common pattern across the globe. *Clim. Res.* **2009**, *38*, 261–263.
56. Hlásny, T.; Sitková, Z. *Spruce Forests Decline in the Beskids*; National Forest Centre, Forest Research Institute Zvolen, Czech University of Life Sciences Prague, Forestry and Game Management Research Institute Jíloviště–Strnady: Zvolen, Czech Republic, 2010.
57. Griess, V.C.; Acevedo, R.; Härtl, F.; Staupendahl, K.; Knoke, T. Does mixing tree species enhance stand resistance against natural hazards? A case study for spruce. *For. Ecol. Manag.* **2012**, *267*, 284–296.

© 2014 by the authors; licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution license (<http://creativecommons.org/licenses/by/3.0/>).