



# Pronounced fluctuations of spruce bark beetle (Scolytinae: *Ips typographus*) populations do not invoke genetic differentiation

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## ABSTRACT

The dynamics of a recent outbreak of the spruce bark beetle (*Ips typographus*) in Switzerland was ruled by a devastating winter storm in 1999 and the drought and heat of the summer 2003. Starting from a similar level of population sizes, estimated as the rate of infested growing stock, beetle populations increased differently in magnitude and time among different regions in Switzerland. Accordingly, we expected local or regional genetic differentiation as a result of such repeated population expansion/breakdown dynamics. We analyzed 5 nuclear microsatellites of spruce bark beetles sampled from pheromone traps at 30 locations distributed over Switzerland. Our genetic results did not indicate any sign of population differentiation, structure, isolation by distance, or recent bottlenecks. This complete lack of genetic structure suggests that spruce bark beetles are highly mobile, precluding the formation of a spatial structure at neutral molecular markers. Thus, this molecular–genetic approach does not allow us to discriminate among regional gene pools and to identify the origin of expanding beetle populations.

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## 1. Introduction

The European spruce bark beetle (*Ips typographus* L.) is one of the economically most important forest insects in Europe (Grégoire and Evans, 2004). It usually attacks Norway spruce trees (*Picea abies* (L.) Karst.) that either recently died or – when living – have a reduced defence system owing to stress. Most often, mass infestations of living trees by the spruce bark beetle occur in stands suffering from the aftermath of heavy winds or from severe drought. Under these conditions spruce bark beetles rapidly develop to extremely high population densities which may result in dramatic mortalities of spruce trees (Meier et al., 2003; Økland and Berryman, 2004; Wermelinger, 2004). Populations usually return to endemic density levels within several years depending on weather conditions, silvicultural situation and control measures (Meier et al., 2003; Wermelinger, 2004). Such changes in population densities may affect the genetic structure of beetle populations owing to genetic drift.

Few studies have investigated the genetic population structure of *I. typographus* using molecular–genetic markers. Mitochondrial (mt) haplotypes showed a distinct geographic structure. One haplotype was restricted to Russian and Lithuanian populations,

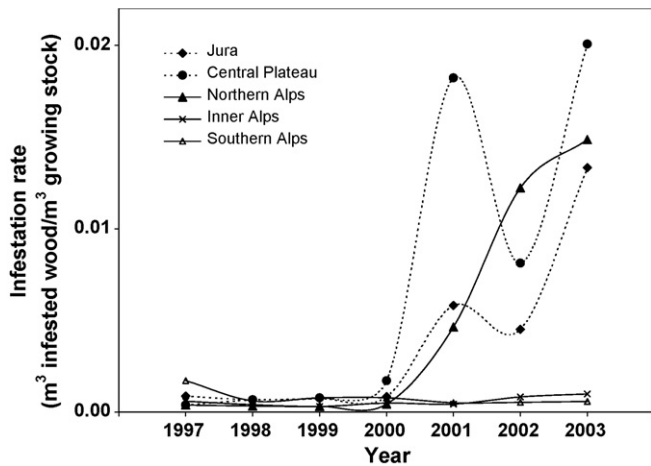
while seven other haplotypes occurred in the rest of Europe at different degrees of admixture (Stauffer et al., 1999). Furthermore, a fixed haplotype was detected in Scandinavia, indicative of a founder effect. An almost homogeneous genetic structure was found across Europe on the basis of nuclear microsatellites (Sallé et al., 2007), but this study included population samples from several years and locations in Europe. This rather homogeneous spatial structure of genetic diversity either suggests that gene flow among European populations of *I. typographus* is high or that effective population sizes are so high that genetic drift does not affect the partitioning of total genetic variation.

In Switzerland, several outbreaks of *I. typographus* occurred during the past 25 years. The devastating storm “Lothar” of 26th December 1999 felled 12.7 million m<sup>3</sup> of timber comprising 82% conifers, mostly spruce (WSL and Buwal, 2001). This triggered an outbreak of *I. typographus* that eventually led to the highest volume of infested timber recorded during the past 200 years in Switzerland. The situation was aggravated by the exceptionally warm and dry year 2003. There were obvious differences in the temporal infestation pattern (Fig. 1), similar to what was observed following an earlier storm (“Vivian”; Engesser et al., 2004), which may be summarized according to the five biogeographical regions in Switzerland (Fig. 2). Before the storm in December 1999, the infestation rates were at a low level all over Switzerland. Conforming to the low amount of windthrown timber in 1999 in the inner and southern Alps (WSL and Buwal, 2001), infestation rates remained constant in these two regions. The Norway spruce

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**Fig. 1.** Fluctuations in Norway spruce (*Picea abies*) infestation rates by the spruce bark beetle (*Ips typographus*) recorded in Swiss forests in five biogeographic regions (Jura mountains, Central Plateau, Northern, Inner and Southern Alps). The storm “Lothar” occurred in December 1999, 2003 was an exceptionally hot and dry year.

stands of the Central Plateau, representing the lowest elevations, were the first to suffer from mass attack. In the second growing season after the storm, infestation rates peaked and thereafter declined again. However, mass attack resumed in the hot and dry summer of 2003, when drought-stressed host trees were again susceptible for infestation. A similar pattern was observed in the Jura mountains except that the peak in 2001 was considerably lower than that of the Central Plateau (Fig. 1). The regional patterns could be attributed to several factors: the wind intensities and therefore storm damage differed between regions. Among the five biogeographical regions, the southern and inner Alps were only weakly affected by the storm as compared to the Jura region, the Central Plateau and the north-western Alps (WSL and Buwal, 2001). The windthrown timber was observed to desiccate more slowly in montane sites and was therefore attractive to beetles over a longer period compared with low-elevation sites (Phyto-

sanitärer Beobachtungs- und Meldedienst PBMD, 2001). Moreover, the summer drought of 2003 was less pronounced in the Alps than in the Central Plateau (Bundesamt für Meteorologie und Klimatologie (MeteoSchweiz), (2004)), and the spruce bark beetles formed one generation per year less in the Alps than at lower elevations (Wermelinger et al., 1999; Forster et al., 2003). These regionally different dynamics emphasise the crucial role of exogenous factors in triggering and governing outbreaks.

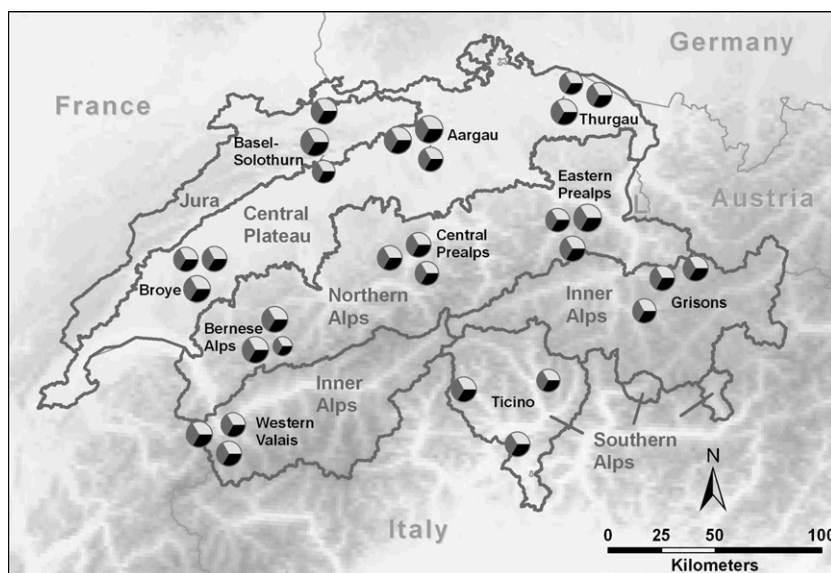
Assuming a homogeneous distribution of genetic variation among the beetle populations in Switzerland before the storm, it could be expected that the huge outbreaks would lead to genetic differentiation of beetle populations owing to genetic drift following the expansion and the subsequent breakdown. Such population fluctuations substantiate the effects of genetic drift, which may lead to strong changes in allele frequencies and eventually to the fixation or loss of alleles. Accordingly, allele frequency-based genetic differentiation among such populations should increase, whereas range expansion – though on a regional scale – could invoke an isolation-by-distance pattern. In this sense, mtDNA analysis showed a fixed haplotype in Scandinavia, which was attributed to a population bottleneck (Stauffer et al., 1999).

Based on the distinct outbreak patterns in the different biogeographic regions of Switzerland (Fig. 1), we addressed the following question: Does the drastic population dynamics of spruce bark beetle in northern Switzerland result in genetic differentiation as a consequence of genetic drift? In other words, do short-term fluctuations of population sizes induce genetic structure? To test this assumption, we sampled beetles from pheromone traps at 30 locations in different regions across Switzerland and analyzed the genetic structure using nuclear microsatellite markers (Sallé et al., 2003).

## 2. Materials and methods

### 2.1. Beetle sampling and processing

In June and July 2004, samples of living bark beetles from pheromone traps at 877 locations were obtained from the forest



**Fig. 2.** Spatial distribution of spruce bark beetle (*Ips typographus*) populations sampled across the five biogeographic regions of Switzerland. Triplets of populations are designated as sub-regions (cf. Table 1). Population assignment, illustrated by the respective shadings in the pie charts, is based on genetic clustering of individuals, exemplified with  $K = 3$  clusters representative of the homogeneous assignment probabilities for all individuals and populations for any number of  $K$ . Chart sizes relate to the number of individuals genotyped per population. Light grey lines and labels refer to neighbouring countries of Switzerland ( $L =$  Liechtenstein), dark grey lines and labels indicate the Swiss biogeographic regions, background shading refers to the topography with light colors for low elevations.

services. Beetles were lyophilized and stored at room temperature until analysis. Out of these samples, we selected 30 locations applying a hierarchical spatial sampling design. These locations represented triplets from ten areas across the five main geographical regions (Table 1, Fig. 2). DNA isolation and genotyping was performed by ecogenics (Zürich-Schlieren, Switzerland). DNA from individual beetles was extracted using a CTAB protocol implemented in the Nuclospin<sup>®</sup> Plant Kit (Macherey-Nagel, Germany). The allelic composition was screened at 5 neutral nuclear microsatellites (ITGT1B6, ITGAA3F10, ITGAA4C3, ITGT343, ITGAA5D8; Sallé et al., 2003) from about 30 individuals per location (Table 1). All 5 markers were amplified in one multiplex-PCR amplification. The 10- $\mu$ L reaction volume contained 2  $\mu$ L of genomic DNA, 0.5  $\mu$ M each of all forward and reverse primers and 5  $\mu$ L of QIAGEN Multiplex PCR Master Mix (with HotStarTaq<sup>®</sup> DNA Polymerase, Multiplex PCR Buffer (6 mM MgCl<sub>2</sub>), and dNTP mix). The following thermotreatment was used: 35 cycles with 94 °C for 30 s, 50 °C for 90 s, and 72 °C for 90 s. Before the first cycle, a prolonged denaturation step (95 °C for 15 min) was included to activate the polymerase, and the last cycle was followed by a 10-min extension. The amplified products were diluted, mixed with internal size standard ET550-R (Amersham Biosciences), run on a MegaBACE

1000 instrument (Amersham Biosciences) and analyzed using Genetic Profiler 2.0 (Amersham Biosciences).

## 2.2. Data analysis

Individual genotypes were retained for statistical analyses if allelic data for at least four loci could be unambiguously determined (958 genotyped individuals in total; Table 1).

We computed basic population genetic parameters using Arlequin 3.11 (Excoffier et al., 2007): expected ( $H_e$ ) and observed heterozygosity ( $H_o$ ) as well as Wright's inbreeding coefficient ( $F_{IS}$ ). Significance of  $F_{IS}$  values was tested by running 1000 permutations. We checked for locus-wise Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LD) within each population using FSTAT (Goudet, 1995).

To test for genetic differentiation, we ran a hierarchical analysis of molecular variance (AMOVA) using ARLEQUIN 3.11. Under the assumptions of random mating within populations and no deviation from HWE, AMOVA partitions the total genetic variation among the hierarchical levels in the model: among groups of populations, among populations within groups, among individuals within populations, and among alleles within individuals. AMOVAs were computed with various groupings of samples (e.g. ten areas

**Table 1**

Sample populations of the spruce bark beetle (*Ips typographus*) in Switzerland, including geographic coordinates, elevations, number of individuals ( $N$ ) genotyped at four to five nuclear microsatellite loci, gene diversity as expected heterozygosity ( $H_e$ ), and inbreeding coefficient ( $F_{IS}$ )

Region and subregion	Local name	Swiss co-ordinates [m]		Elevation [m a.s.l.]	$N$	$H_e^a$	$F_{IS}$
		Easting	Northing				
Jura (J) and Central Plateau (CP)							
Basel–Solothurn (J)	Farnern	612,500	235,550	940	30	0.524	−0.006
	Nunningen	611,800	250,400	680	35	0.516	0.031
	Schelten	607,900	241,400	1080	36	0.537	0.054
Broye (western CP)	Surpierre	555,050	177,575	690	30	0.507	0.081
	Lovatens	556,720	171,200	790	37	0.496	−0.047
	Montagny-les-Monts	564,200	184,100	650	29	0.520	−0.048
Aargau (central CP)	Büttikon	662,400	243,100	510	34	0.472	0.079
	Hägglingen	661,200	250,500	510	36	0.468	0.004
	Egliswil	656,000	245,000	510	32	0.504	−0.016
Thurgau (eastern CP)	Weinfelden	723,500	269,500	420	32	0.519	0.074
	Alterswilen	729,570	276,020	530	34	0.496	0.101*
	Hefenhofen	740,000	271,000	470	29	0.522	−0.018
Northern Alps							
Bernese Alps	Gstaad	588,905	144,270	1540	32	0.509	0.005
	Zweisimmen	594,154	156,534	1280	27	0.546	−0.061
	Lenk	598,389	145,384	1400	38	0.505	0.031
Central Prealps	Melchtal	664,025	184,075	1060	27	0.519	−0.027
	Giswil	651,700	189,660	1300	29	0.475	0.175**
	Sarnen	659,400	196,175	1200	32	0.551	−0.021
Eastern Prealps	Engi	730,400	206,150	1200	34	0.484	0.067
	Flumserberg	737,875	213,125	1500	39	0.515	−0.036
	Elm	731,650	198,450	1140	30	0.494	−0.053
Inner (IA) and Southern Alps (SA)							
Western Valais (IA)	La Forclaz	567,500	102,250	1400	40	0.506	−0.078
	Vollèges	577,600	105,280	1580	32	0.494	0.065
	Orsières	576,250	93,700	1260	31	0.560	−0.014
Grisons (IA)	Klosters	789,890	192,630	1320	33	0.494	0.063
	Langwies	774,500	187,225	1720	31	0.509	−0.039
	Brienz (GR)	766,980	171,500	1200	31	0.463	0.040
Ticino (SA)	Cerentino	684,560	130,060	1240	27	0.541	0.043
	Val Pontirone	723,900	136,500	1540	19	0.528	−0.100
	Mezzovico	711,140	105,890	1340	32	0.515	0.017

Triplets of populations are grouped according to spatial proximity. \* $P < 0.05$ , \*\* $P < 0.01$ .

<sup>a</sup> Mean of four to five nuclear microsatellite loci is given. None of the  $H_e$  values significantly deviated from mean observed heterozygosity ( $H_o$ ).

with three populations or three geographic regions similar in population dynamics; Figs. 1 and 2). Pairwise population differentiation ( $\Phi_{ST}/(1 - \Phi_{ST})$ ;  $\Phi_{ST}$  as an analogue of  $F_{ST}$ ) was calculated and used for a Mantel matrix correlation with geographic distance to test for isolation by distance. For significance tests in AMOVAS, pairwise population differentiation and the Mantel test, we ran 1000 permutations.

To infer population structure, we applied the Bayesian model implemented in Structure 2.0 (Pritchard et al., 2000). This model assigns individuals and populations to a number of  $K$  clusters. We allowed for population admixture and correlated allele frequencies, setting a uniform prior for the level of admixture  $\alpha = 1.0$  and, based on the above analyses, a general population differentiation at  $F_{ST} = 0.01$  (50,000 burn-in periods, 100,000 Markov chain Monte Carlo repetitions). The analysis was iterated three times for each  $K = 2-10$ .

We further used BOTTLENECK 1.2.02 (Cornuet and Luikart, 1996) to test for recent bottlenecks. A bottleneck should reduce allele number more strongly than heterozygosity  $H_e$ . If  $H_e$  is significantly larger than the heterozygosity expected based on a mutation-drift equilibrium ( $H_{eq}$ ), this indicates that the population has experienced a strong reduction in population size, i.e. a bottleneck, only few generations ago. As suggested by the software authors, we ran 1000 iterations to determine significance levels under both the infinite allele model (IAM) and the two-phased mutation model (TPM; for details see the manual).

### 3. Results

The 5 nuclear microsatellite loci revealed 8–14 alleles, which showed skewed frequency distributions with 1 or 2 dominant alleles in all but 1 locus (ITGAA5D8; data not shown). Gene diversity ( $H_e$ ) ranged from 0.463 to 0.560 per population (Table 1). Inbreeding coefficients ( $F_{IS}$ ) varied from  $-0.100$  to  $0.175$  within populations, with only 2 out of the 30 samples showing a significant homozygote excess (locations Alterswilten and Giswil; Table 1). The data revealed no deviation from HWE per locus and population and no LD.

We found that within-population variation accounted for practically 100% of total genetic variation, while no variation was explained by among-group or among-population variation, independent of the type of grouping chosen (for an example see Table 2). Likewise, only 28 (6.4%) out of 435 pairwise  $\Phi_{ST}$  values were significant at  $P = 0.05$ . We detected no isolation by distance pattern (Mantel  $r = -0.051$ ;  $P = 0.761$ ).

Each individual and, accordingly, each population showed an even probability to be assigned to either of  $K$  gene clusters, independent of the number of clusters ( $K = 3$  as example in Fig. 2). There was no indication of a most likely value of  $K$  based on the log-likelihood of assignment (data not shown). None of the 30 populations sampled showed signs of a recent bottleneck. Only in 4 out of 300 tests (30 populations  $\times$  5 loci  $\times$  2 models) was  $H_e$  significantly higher than  $H_{eq}$ .

**Table 2**

Partitioning of total genetic variation assessed for 5 nuclear microsatellite loci in 30 Swiss populations of spruce bark beetle (*I. typographus*)

Source of variation	d.f.	SS	% variation
Among groups	2	2.4	-0.01
Among populations within groups	27	35.1	0.04
Among individuals within populations	1886	2393.4	99.98

Grouping refers to the five main biogeographic regions of Switzerland (see Table 1, Fig. 1). None of the percentages were significant at  $P = 0.05$ , d.f.: degrees of freedom, SS: sums of squares.

## 4. Discussion

### 4.1. Population genetic structure

Because of the pronounced population fluctuations in the spruce bark beetle at the beginning of the 21st century (Fig. 1), we expected to detect distinct regional genetic differentiation among populations from regions characterized by different population dynamics, i.e. between those where population sizes varied dramatically or remained relatively constant. However, our molecular-genetic data indicate that none of the study populations showed any sign of neither increased differentiation nor a population bottleneck: the genetic structure in the Swiss spruce bark beetle populations was virtually absent, i.e. it was not possible to reasonably group populations into (regional) spatial clusters (STRUCTURE; Fig. 2), there was no significant partition of among-group variation (AMOVA; Table 2), and we found no isolation by distance (Mantel correlation). We therefore assume that populations of spruce bark beetle were always large enough to buffer against genetic drift. Alternatively, quick homogenisation through extensive gene flow via long-distance dispersal and large-scale random mating blurred short-term demographic effects on population genetic parameters. Nei et al. (1975) argue that the reduction in heterozygosity is small in populations rapidly growing after a bottleneck, which would make it difficult to detect such a random sampling effect. On the other hand, extreme mobility of spruce bark beetles is likely to cause the regional spread of infestation frequently observed during mass reproduction. The complete absence of population differentiation found supports the notion of extensive gene flow and random mating across the entire study range. This high mobility also precludes the molecular identification of local or regional source populations during a population expansion phase following mass reproduction. Our results were in agreement with the few other existing genetic data on spruce bark beetle, suggesting a uniform genetic structure of this species even at the European level (Stauffer et al., 1992; Sallé et al., 2007). The fact that the STRUCTURE analysis did not allow us to find any population grouping at first let us assume that this was due to isolation by distance, as indicated by the software's authors Pritchard et al. (2007; 2004 is an older version). In such a situation, an optimal number of  $K$  clusters is difficult to find because allele frequencies vary gradually and most individuals will show mixed cluster membership (probability of  $1/K$ ). However, the Mantel matrix correlation test, which was not significant, clearly contradicted this, suggesting that the sample populations lack any genetic structure whatsoever. The latter does not conform to the study of bark beetle populations across Europe, in which a weak trend to isolation by distance was observed (Sallé et al., 2007). We assume that the spatial expansion of our study range was too small to indicate such a gradient in population differentiation. Such an explanation is supported by the fact that a singular maternal lineage of the predominant host tree of *I. typographus*, *Picea abies*, successfully re-colonized the entire Western Alps that led to a practically uniform mtDNA haplotype occurrence (Gugerli et al., 2001; Tollefsrud et al., unpublished data). Sallé et al. (2007) tested whether this pair of host and parasite might show a congruent phylogeographic structure, but they had to reject this hypothesis. It seems that the occurrence of host tree populations or environmental barriers to gene flow rather than common migration determine the genetic structures of associated organisms, as has been shown in *Dendroctonus ponderosae* and *Pinus* spp. (Mock et al., 2007).

Our genetic data suggest high mobility of the spruce bark beetles. This notion is also supported by experimental data (cf. Sauvard, 2004). Beetles are known to disperse over long distances

either actively (Gries, 1985) and/or by wind (Forsse and Solbreck, 1985). Active flight distances calculated from fat reserve consumption reach up to 19 km (Gries, 1985). Wind-supported active flight of only 1 h moves beetles approximately 18 km (Forsse and Solbreck, 1985). Another indication for intense dispersal was found in a mark-release-recapture study in which considerable quantities of unmarked beetles were caught in a pine forest with the next spruce forest being at least at 6 km distance (Duelli et al., 1997). Based on our data and those of Sallé et al. (2007), we argue that strong gene flow over relatively short time periods (few generations) prevents the formation of a genetic structure in *I. typographus*. Our study specifically indicates that not even the high mountains of the Alps represent a topographical barrier for these insects.

#### 4.2. Consequences for forest management

Addressing the question about the origin of the infesting beetles, the genetic discrimination between different neighbouring populations of bark beetles might be very useful. Accordingly, a practical aspect of our study was to test if molecular–genetic analyses enable us to identify the origin of *I. typographus* populations and resulting outbreaks. The genetic discrimination of local or regional populations of *I. typographus* would be a valuable tool in bark beetle management. It would allow one to discern local and neighbouring populations, to identify migration capacities and to define buffer zones between managed and unmanaged stands. However, given the extreme mobility of *I. typographus* inferred from population genetic data, it is evident that populations cannot be discriminated, neither on a local nor regional scale, even following strong population fluctuations that favour genetic drift.

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