



Colonisation of native and exotic conifers by indigenous bark beetles (Coleoptera: Scolytinae) in France

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ABSTRACT

Planting exotic conifers offers indigenous forest insects an opportunity to extend their host range and eventually to become significant pests. Knowing the ecological and evolutionary modalities driving the colonisation of exotic tree species by indigenous insects is thus of primary importance. We compared the bark beetle communities (Coleoptera: Curculionidae, Scolytinae) associated with both native and introduced conifers in France. The aim of our study was to estimate the influence of both host- and insect-related factors on the beetles' likelihood to shift onto new hosts. We considered the influence of host origin (i.e. native vs. exotic), host tree species identity, tree bark thickness and tree taxonomic proximity, as well as insects' host specificity. A field inventory using trap trees was carried out in two regions in France (Limousin and Jura) during two consecutive years (2006 and 2007) on three European native conifer species [Norway spruce (*Picea abies*); Scots pine (*Pinus sylvestris*) and European Silver-fir (*Abies alba*)] and five North American [Sitka spruce (*Picea sitchensis*); Eastern white pine (*Pinus strobus*); Grand fir (*Abies grandis*); Douglas fir (*Pseudotsuga menziesii*) and Western red cedar (*Thuja plicata*)]. A total of 18 indigenous and 2 exotic bark beetle species were collected. All exotic conifer species were colonised by indigenous bark beetle species and no significant difference was observed of the cumulated species richness of the latter between native and exotic tree species (13 vs. 14, $P < 0.05$). The ability of indigenous bark beetles to shift onto exotic conifers appeared to strongly depend on host species (significantly structuring bark beetle assemblages), the presence of phylogenetically related native conifer species and that of similar resources, in combination with insect host specificity. Host tree species status (native or exotic) also seemed to be involved, but its effect did not seem as essential as that of the previous factors. These findings are discussed in terms of adaptation, plasticity and practical aspects of forest management.

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1. Introduction

During the last century, European forests have undergone important changes following the introduction of exotic conifers intended to increase forest plantation productivity for wood exploitation (Zobel et al., 1987). These introduced species were mainly Pinaceae from North America because of their excellent economic features (i.e. large size and rapid growth) such as Lodgepole pine, *Pinus contorta* Doug. ex. Loud. var. *latifolia* Engelm., Sitka spruce, *Picea sitchensis* (Bong.) Carrière, and Douglas fir, *Pseudotsuga menziesii* (Mirb.) Franco (Boyce, 1954). Nowadays,

these large plantations represent a significant contribution to forest ecosystems in Europe, which may have altered, in particular, trees–insects relationships (Lieutier, 2006). The presence of novel hosts offers indigenous insects an opportunity to extend their host range and eventually to become significant pests. As a result, exotic tree species may sometimes be more prone to insect outbreaks than native tree species (Boyce, 1954; Zobel et al., 1987). Consequently, it is crucial to first understand the ecological and evolutionary modalities which drive the colonisation of exotic tree species by indigenous insects.

Studies comparing the susceptibility of exotic and native conifers to phytophagous insects have given contrasted results so far. Newly introduced conifers are often more colonised than native species but opposite conclusions have been reported as well (Bejer, 1981; Delplanque et al., 1987; Evans, 1987; da Ros et al., 1993; Fraser and Lawton, 1994; Lindelöw and Björkman, 2001; Dalin and Björkman, 2006; Lieutier, 2006; Roques et al., 2006).

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Several factors can facilitate or constrain host shift and establishment success of indigenous insects on a new host. These factors are often linked to plant characteristics: abundance (Neuvonen and Niemelä, 1981), geographical range (Strong, 1974), age of introduction (Kennedy and Southwood, 1984), tree size and structural complexity (Lawton and Schroder, 1977), taxonomical or resource proximity (Ehrlich and Raven, 1964; Connor et al., 1980) and defence mechanisms (Lieutier, 2006). Insect characteristics, such as host specificity (Fraser and Lawton, 1994), the degree of intimacy with the host tree (Lieutier, 2006) and lack of natural enemies (Keane and Crawley, 2002) can also affect host shift ability. Among these different factors, tree taxonomic proximity among natural and novel hosts and insects' host specificity often have a strong influence on insect establishment on new conifer species, with some variations depending on sites and species studied (Evans, 1987; Lindelöw and Björkman, 2001; Dalin and Björkman, 2006; Lieutier, 2006; Roques et al., 2006).

The interactions between conifers and bark beetles (Coleoptera: Curculionidae, Scolytinae) are of major importance for forest ecosystems, because these insects play both ecological and economical key roles in forest management (Grégoire and Evans, 2004). However, in Europe few studies have investigated their ability to establish onto exotic conifers, and they have generally focused on only one bark beetle species (Zumr, 1992; Langström et al., 1995; Amezaga, 1996; Brocknerhoff et al., 2006; Lombardero et al., 2008). European conifer bark beetles form a homogenous ecological group of species generally specialists of one tree genus within Pinaceae. Host selection is performed by dispersing adult pioneer beetles and is probably based on visual and olfactory signals from host trees (Byers, 2004; Campbell and Borden, 2006), as well as host physical properties like bark thickness (Paine et al., 1981; Amezaga and Rodríguez, 1998; Bertheau et al., in press). Once they have selected a host, and eventually depleted its defence mechanisms, beetles mate and lay their eggs within host tissues where all larval development occurs (Sauvard, 2004). Therefore, bark beetles show a high level of interaction and a high intimacy with their host trees, implying a high degree of adaptation. Nonetheless, bark beetles exhibit also a certain level of plasticity in selection and performances among different hosts, which make them very likely to colonise tree species beyond their ordinary host range. They have often been observed/have often been seen to attack trees belonging to another genus, closely related to their usual hosts. For example, *Ips typographus* (L.) and *Pityogenes chalcographus* (L.) can develop in *Pinus*, *Abies* and *Larix* species while *Picea* species are the most common hosts (Chararas, 1962). Likewise, indigenous bark beetles have also been observed on introduced Pinaceae species, often congeners of their usual host (Evans, 1987; Lindelöw and Björkman, 2001), but even Douglas fir has been reported to be colonised although it lacks native congeners in Europe (Legrand, 1997). Knowing the factors that favour these host shifts would give useful information to build effective monitoring and control methods in European conifer forests, where planting of exotic tree species has increased in many regions.

The aim of the present study was to estimate to which extent tree- and insect-related factors affected bark beetles' ability to shift onto exotic host conifers. We investigated in particular the influence of the following factors: (1) host origin (i.e. native vs. exotic), (2) host tree species identity, (3) tree bark thickness, (4) tree taxonomic proximity and (5) insect host specificity on the bark beetle communities associated with conifers in France. We performed a two-year field inventory of bark beetles species colonising three native and five exotic conifer species in France. We surveyed the bark beetle community and species richness associated to each host tree and assessed whether their variations were affected by the different tree-related factors considered. We

also established bark beetles' host specificity and investigated whether it was related to their occurrence on exotic hosts.

2. Material and methods

2.1. Conifer species and study areas

Three European native and five North American exotic conifer species, from the Pinophyta division were selected to carry out analyses by taking into account various taxonomic relationships: intra-generic, intra-familial and interfamilial levels. The native species were Norway spruce, *Picea abies* L. Karst.; Scots pine, *Pinus sylvestris* L. and European Silver-fir, *Abies alba* Mill., while the exotic species were *P. sitchensis*; Eastern white pine, *Pinus strobus* L.; Grand fir, *Abies grandis* Douglas ex (D. Don) Lindl. and *P. menziesii*. All these tree species belonged to the Pinaceae family. The Western red cedar, *Thuja plicata* Donn ex D. Don., an exotic Cupressaceae species was also considered.

To ensure a certain level of diversity in both conifer and bark beetles species, the study was undertaken over two consecutive years (2006 and 2007) and in two regions (the Limousin and Jura). All exotic species have been present in these regions for approximately 60 years. Although the Limousin is located in the centre of France and Jura in the North-East, the climatic conditions in 2006 and 2007 were similar in both regions (mean temperatures during 2006 and 2007: the Limousin: October–March: 5 °C, April–September: 14 °C; Jura: October–March: 5 °C, April–September: 16 °C; average rainfall in 2006 and 2007, respectively: the Limousin 96 and 103 mm, Jura: 71 and 69 mm). In the Limousin, where forest areas are dominated by *P. abies* and *P. menziesii*, 11 plots were selected within three plantation forests (St Pierre-Bellevue, Chamboux and Larfeuil), each plot being a pure stand of a single tree species. In Jura, 12 plots were considered in two forest sites (Chaux and Montbarrey). *P. sylvestris* was the dominant conifer species but stands were often mixed with several broad-leaved tree species. The main geographic and silvicultural characteristics of the plots are presented in Table 1.

2.2. Sampling method and bark beetle species identification

In each plot, beetles were collected on trap trees which had either been felled or selected after windfalls. For each tree, the upper part of the trunk and the branches were removed. Age, diameter (at 1 m above ground) and height were measured (see Table 1). In 2006, trees were felled at two different dates in order to have trees at different decaying stage and thus increase the probability of attracting a wide array of bark beetle species. Felling dates differed between the two regions since, because of their remoteness, plots were not accessible at the same period in winter. One to four trees per plot were felled. Two bark pieces (8 dm² each) were randomly sampled from the trunk of each tree, at least 50 cm apart from each other. In 2007, two trees were felled at the end of February, prior to the bark beetles' swarming period and the number of bark pieces sampled was increased to 10 per tree (1 dm² each), separated by at least 25 cm from each other to get a better coverage of the trunk. During the two years, each tree was sampled once a month, from April to September, corresponding to the period of bark beetles' activity. Each sample was placed into a plastic bag and transported to the laboratory. Bark beetles were then extracted from the samples, by removing bark layers, and placed into 100% ethanol for identification. At the same time, bark thickness measurements were made with callipers at two points for each bark sample. Adults were identified to species level using Balachowsky's key (Balachowsky, 1949) and identifications were checked by the Entomological section of the French Forest Service (Office National des Forêts).

Table 1Characteristics of the plots and trap trees in the Limousin (L) and Jura (J) (means \pm standard errors).

Tree species	Forest plots	Latitude	Longitude	Altitude (m)	Density (trees/ha)	Trap tree age (years)	Trap tree diameter (m)	Trap trunk height (m)	Nb. trap trees		Date of cutting		
									2006	2007	2006	2007	
European native tree species													
<i>Picea abies</i>	Chamboux (L)	45N40'64"	2E00'45"	796	–	28.67 ± 1.73	0.35 ± 0.10	8.98 ± 1.04	4	2	November 2005 to May 2006	February 2007	
<i>Picea abies</i>	Larfeuil (L)	45N30'78"	1E57'75"	796	793	37.33 ± 2.30	0.35 ± 0.08	14.91 ± 1.11	4	2	November 2005 to May 2006	February 2007	
<i>Picea abies</i>	St Pierre Bellevue (L)	45N54'33"	1E53'75"	637	1200	28.00 ± 2.00	0.23 ± 0.03	10.02 ± 2.20	2		November 2005 to May 2006	–	
<i>Picea abies</i>	Chaux (J)	47N04'48"	5E31'44"	225	>650	30.33 ± 1.71	0.39 ± 0.09	13.75 ± 0.93	4	2	May 2006 to July 2006	February 2007	
<i>Picea abies</i>	Montbarrey (J)	47N01'68"	5E37'00"	240	>600	30.75 ± 0.75	0.54 ± 0.15	13.45 ± 1.29	2	2	May 2006 to July 2006	February 2007	
<i>Pinus sylvestris</i>	Chamboux (L)	45N40'04"	2E00'68"	793	–	22	0.25	11	1		November 2005	–	
<i>Pinus sylvestris</i>	St Pierre Bellevue (L)	45N54'27"	1E54'47"	693	1910	32.33 ± 2.74	0.38 ± 0.11	9.57 ± 0.69	4	2	November 2005 to May 2006	February 2007	
<i>Pinus sylvestris</i>	Chaux (J)	47N02'99"	5E42'84"	245	>700	30.67 ± 2.22	0.46 ± 0.13	12.22 ± 1.23	4	2	May 2006 to July 2006	February 2007	
<i>Pinus sylvestris</i>	Chaux (J)	47N02'27"	5E33'38"	227	>650	32.33 ± 2.44	0.33 ± 0.11	15.02 ± 0.31	4	2	May 2006 to July 2006	February 2007	
<i>Abies alba</i>	Chaux (J)	47N04'34"	5E32'83"	250	>700	38.17 ± 1.14	0.36 ± 0.14	15.13 ± 1.29	4	2	May 2006 to July 2006	February 2007	
<i>Abies alba</i>	Chaux (J)	47N03'48"	5E42'78"	245	>600	37.00 ± 1.15	0.40 ± 0.09	12.53 ± 0.97	4	2	May 2006 to July 2006	February 2007	
North-American exotic tree species													
<i>Picea sitchensis</i>	Chamboux (L)	45N41'18"	2E01'72"	801	–	26.17 ± 1.19	0.44 ± 0.11	12.92 ± 0.49	4	2	May 2006 to July 2006	February 2007	
<i>Picea sitchensis</i>	Larfeuil (L)	45N30'53"	1E57'24"	771	793	28.50 ± 3.01	0.48 ± 0.12	16.92 ± 1.05	4	2	November 2005 to May 2006	February 2007	
<i>Pinus strobus</i>	Chaux (J)	47N02'38"	5E35'11"	243	>700	29.33 ± 2.17	0.44 ± 0.08	14.53 ± 0.86	4	2	May 2006 to July 2006	February 2007	
<i>Abies grandis</i>	Larfeuil (L)	45N32'68"	1E58'30"	882	561	37.50 ± 1.19	0.46 ± 0.11	17.50 ± 1.06	2	2	November 2005 to May 2006	February 2007	
<i>Abies grandis</i>	Chaux (J)	47N02'03"	5E38'59"	248	>200	34.50 ± 1.85	0.41 ± 0.04	14.08 ± 1.89	4	2	May 2006 to July 2006	February 2007	
<i>Abies grandis</i>	Chaux (J)	47N04'36"	5E33'72"	250	>700	32.17 ± 1.35	0.46 ± 0.11	13.34 ± 0.57	4		May 2006 to July 2006	–	
<i>Pseudotsuga menziesii</i>	Chamboux (L)	45N40'92"	2E01'69"	812	–	33.33 ± 2.72	0.51 ± 0.13	17.90 ± 0.66	4	2	November 2005 to May 2006	February 2007	
<i>Pseudotsuga menziesii</i>	Larfeuil (L)	45N29'86"	1E57'87"	821	447	33.40 ± 2.18	0.51 ± 0.16	18.60 ± 0.43	3	2	November 2005 to May 2006	February 2007	
<i>Pseudotsuga menziesii</i>	St Pierre Bellevue (L)	45N54'90"	1E53'84"	637	520	39.00 ± 0.91	0.58 ± 0.16	15.73 ± 4.21	2	2	November 2005 to May 2006	February 2007	
<i>Pseudotsuga menziesii</i>	Chaux (J)	47N02'31"	5E33'41"	227	>650	35.83 ± 1.54	0.57 ± 0.16	16.05 ± 0.59	4	2	May 2006 to July 2006	February 2007	
<i>Pseudotsuga menziesii</i>	Montbarrey (J)	47N00'30"	5E37'73"	235	>600	32.75 ± 3.42	0.52 ± 0.10	15.88 ± 0.72	2	2	May 2006 to July 2006	February 2007	
<i>Thuja plicata</i>	Chaux (J)	47N04'39"	5E30'01"	223	>450	42.50 ± 1.05	0.52 ± 0.13	16.63 ± 0.79	4	2	May 2006 to July 2006	February 2007	

2.3. Data analysis

Analyses were based on the presence or absence of bark beetle species in the plots, each plot corresponding to a particular tree species. Bark beetle species were considered present in a plot if at least one adult was found within a gallery system in a sample. Cumulated species richness was calculated on native and exotic trees because we considered that it allowed the total rate of recruitment by these two tree categories to be approached.

To ensure our data was consistent among years and regions, comparisons were carried out between years for each region and between regions for each year, but only the tree species common to the two regions were considered in the between-regions comparisons. The cumulated species richness was compared by means of a randomization test following Manly (Manly, 1997) with 1000 randomizations. A confidence interval for the cumulated species richness was assessed by bootstrap based on 1000 replicates (Manly, 1997). The cumulated bark beetle species richness in native and exotic tree species was also compared, the same way as described above.

Raw data were analyzed by a correspondence analysis (CoA) in order to unravel the host tree–bark beetle co-occurrence. We analyzed the impact of host origin, host species and bark thickness classes upon the pattern of bark beetles species occurrence by mean of the between-class CoA. The principle of this analysis is to quantify the between classes multivariate variability, the classes being defined as groups of either host tree origin or species or bark thickness classes. The between classes CoA therefore focuses on group differences and allows for the testing of its statistical significance by means of a randomization procedure. The CoA and the between class tests were done using the software R (R Development Core Team, 2008) and the R package ade4 (Chessel et al., 2004). With regards to bark thickness, each tree species was characterised by two mean values measured from the samples: bark thickness at 1/10th and at 9/10th of the trunk height. Using these two parameters, similarities among host species were quantified by Euclidean distances and represented by an unweighted pair group mean average (UPGMA) tree clustering. Thus, in the between classes CoA, bark thickness groups were selected according to similarities among tree species.

To test the taxonomic proximity factor, the similarities between bark beetle communities were calculated using the Sørensen's quotient of similarity $QS = 2c/(a + b)$, in which 'a' represents the number of bark beetle species on host A, 'b' the number of species on host B and 'c' the number of species shared by A and B (Sørensen, 1948). Results were summarized by an UPGMA tree clustering based on Sørensen's distances ($1 - QS$). The resulting classification was compared to a similar tree based on DNA similarity. We built the tree species phylogeny using DNA sequences of the ribulose-biphosphate-carboxylase (*rbcl*) gene published in the GenBank database (GenBank accession numbers: AB097775, AB019798, AB019825, X63660, AB029652, AB029646, AF127428 and X52937). The sequences were aligned using Clustal W (Thompson et al., 1994) as implemented in BioEdit, and a Neighbor Joining (NJ) analysis, based on Kimura 2 Parameter genetic distances (Kimura, 1980), was performed using Mega4 (Tamura et al., 2007). The robustness of the tree branches was assessed by bootstrap (100 replicates).

We examined if there was a relationship between the observed host range of bark beetle species and their propensity to colonise exotic tree species. This was done by examining the correlation coefficient (Pearson's coefficient r) between the percentage of colonised exotic tree species and the percentage of colonised native tree species. We assumed that a bark beetle species that was able to colonise many native tree species was also able to colonise many exotic tree species.

All variables were checked for their homoscedasticity (Levene test) and normal distribution (Shapiro–Wilk test). All statistical tests were considered significant at $P \leq 0.05$. Means are given with their standard error (SE).

3. Results

The randomization tests indicated no significant difference of the cumulated species richness between regions either in 2006 or 2007 (2006: 9 vs. 11; 2007: 14 vs. 12, in the Limousin and Jura, respectively). The inter-annual difference in the species richness was not significant in the Limousin (11 vs. 12 in 2006 and 2007, respectively) while a significant difference was observed in Jura (9 vs. 14 in 2006 and 2007, respectively, $P < 0.05$). Further analyses were based on pooled data from both regions and years.

3.1. Bark beetle species distribution and richness

Twenty bark beetle species were recorded in total (Table 2), among which two were exotic: *Gnathotrichus materiarius* Fitch. from North America and *Xyleborus germanus* Bland. from Japan. Because the study focused on the colonisation processes of exotic trees by indigenous bark beetle species, these two species were excluded from the analyses. Five beetle species, *Hylastes cunicularius* Erich., *Ips acuminatus* Gyll., *Pityokteines curvidens* Germ., *Pityophthorus pityographus* Ratz., and *Xyleborus saxesenii* Ratz. were collected in only one or two samples in only one plot. They were thus taken into account for further species richness calculations, but were excluded from the other analyses because we considered they were too rare to correctly infer their distribution among tree species.

P. sylvestris and *P. abies* recruited altogether 78% of the bark beetle species. Most beetle species collected on exotic conifers were also collected on native trees, but *P. curvidens*, *Pityokteines spinidens* Reit. and *P. pityographus* colonised only *A. grandis*. *P. chalcographus* and *I. typographus* colonised all Pinaceae species, and *P. chalcographus* also colonised *T. plicata*. *Cryphalus piceae* Ratz., *Dryocoetes autographus* Ratz. and *Xyloterus lineatus* Oliv. colonised several but not all Pinaceae genera, while the other bark beetles were restricted to one or two genus and *Tomicus piniperda* was collected on *P. sylvestris* only.

A total of 14 and 13 bark beetle species was encountered on native and exotic tree species, respectively. The randomization test indicated that this difference was not significant ($P < 0.05$; Table 2).

3.2. Comparison of bark beetle communities

The inertia of the general CoA was 1.9 and the two first axes accounted for 28 and 16% of the total inertia, respectively.

First, there was a clear separation between native (*P. sylvestris*, *P. abies* and *A. alba*) and exotic (*P. menziesii*, *A. grandis*, *P. sitchensis*, *P. strobus* and *T. plicata*) host tree species (Fig. 1). The randomization procedure indicated that this difference was significant at $P < 0.039$ (1000 randomizations). The between host origin inertia was 0.16, representing 8.4% of the total inertia. Secondly, host species identity also strongly affected the distribution of the bark beetle species as indicated in Fig. 2a. The between-host difference was tested by means of 1000 randomizations and was significant at $P < 0.016$. The first axis separated *Pinus* and *Picea* species from *Abies* species, with *P. menziesii* and *T. plicata* at an intermediate position. In the *Picea*–*Pinus* group however, *P. sylvestris* was isolated from the other *Pinus* species and from the *Picea* species by the second axis. Fig. 2b shows the projection of the bark beetle species upon the plane defined by axes 1 and 2 of the CoA. Axis 1 separated bark beetle species in two groups, *C. piceae* and

Table 2

Presence and specific richness of bark beetle species collected on native (N) and exotic (E) conifers species, gathering data from different plots in the Limousin and Jura.

Bark beetle species	<i>Picea abies</i> (N)	<i>Picea sitchensis</i> (E)	<i>Pinus sylvestris</i> (N)	<i>Pinus strobus</i> (E)	<i>Abies alba</i> (N)	<i>Abies grandis</i> (E)	<i>Pseudotsuga menziesii</i> (E)	<i>Thuja plicata</i> (E)	Total native tree species colonised	Total exotic tree species colonised
Species used in the analyses										
<i>Cryphalus piceae</i> Ratz.			•		••	•••	••		2	2
<i>Crypturgus cinereus</i> Herb.	••		•						2	0
<i>Crypturgus pusillus</i> Gyll.	•••		••	•					2	1
<i>Dryocoetes autographus</i> Ratz.	••••	••	••	•			•		2	3
<i>Hylurgops palliatus</i> Gyll.	••••	••	••••						2	2
<i>Ips sexdentatus</i> Boern.			••••	•			•		1	2
<i>Ips typographus</i> L.	•••••	••	••	•	•	•	•		3	4
<i>Orthotomicus erosus</i> Woll.	•		••						2	0
<i>Orthotomicus laricis</i> Fabr.	•		••				•		2	1
<i>Pityogenes chalcographus</i> L.	•••••	••	•••	•	•	•••	•••	•	3	5
<i>Pityokteines spinidens</i> Reit.						•			0	1
<i>Tomicus piniperda</i> L.			••••						1	0
<i>Xyloterus lineatus</i> Oliv.	•		•				•		2	1
Rare species										
<i>Hylastes cunicularius</i> Erich.	•									
<i>Ips acuminatus</i> Gyll.			•							
<i>Pityokteines curvidens</i> Germ.						•				
<i>Pityophthorus pityographus</i> Ratz.						•				
<i>Xyleborus saxesenii</i> Ratz.							•			
Exotic species										
<i>Gnathotrichus materiarius</i> Fitch.			•	•			•			
<i>Xyleborus germanus</i> Bland.	••		•	•	•	•	•			
Cumulated species richness (without exotic beetles)	10	4	13	6	3	6	8	1	14	13
Mean species richness (bootstrap)									13	10.4
Lower bound of the 95% confidence interval of the mean species richness (bootstrap)									11	8
Upper bound of the 95% confidence interval of the mean species richness (bootstrap)									14	13

The number of dots (•) indicates the number of plots where the bark beetles were recorded. Comparison of the cumulated species richness between the native and exotic tree species colonised was assessed by means of randomization test and bootstrap confidence interval, $P < 0.05$.

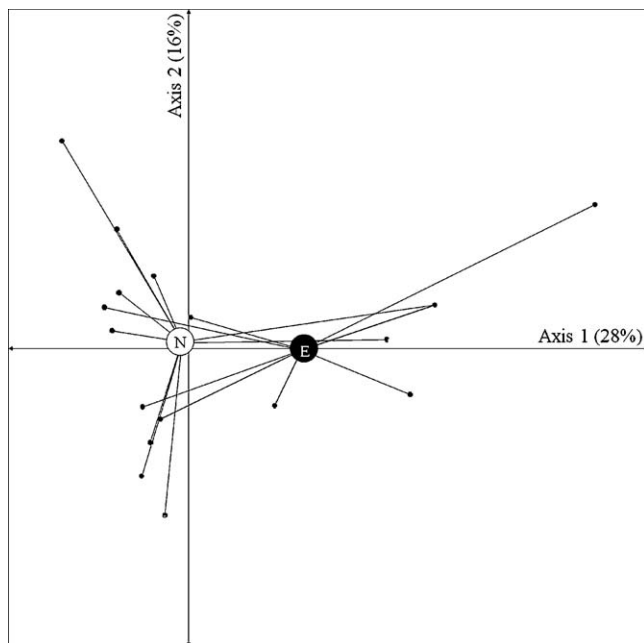


Fig. 1. Factorial correspondence analysis (CoA) of the bark beetle species occurrence on different native and exotic conifer species. Projection of the sampled trees upon the axes 1 and 2 of the CoA. Points are grouped by the host origin (native vs. exotic). The white circle is placed at the gravity centre of the native host species and the black circle at the gravity centre of the exotic host species. Lines indicate links between gravity centres and their corresponding samples.

P. spinidens in one and all other species in the other. Axis 2 accounted for differences in the frequency of several species among which *T. piniperda*, *O. erosus* and *C. cinereus* appeared as the most important. The between host species identity inertia was 0.87, representing 46% of the total inertia.

Euclidean distances and the tree clustering method distinguished three groups of conifer species according to their similarities in bark thickness (Fig. 3a): a first group with *A. grandis* and *T. plicata* (BT1) linked to the second group including *A. alba*, *P. strobus*, *P. abies* and *P. sitchensis* (BT2) and a third group with *P. sylvestris* and *P. menziesii* (BT3). We tested the effect of these groups upon the raw data inertia using the between class inertia test used above. The randomization procedure indicated a highly significant effect of these groups ($P < 0.001$). The first axis separated BT1 group from BT2 and BT3 groups (Fig. 3b). The BT3 group was isolated from the BT2 group by the second axis. The between host species identity inertia was 0.45, representing 24% of the total inertia.

3.3. Role of the tree taxonomic proximity

The dendrogram built from the Sørensen's quotient of similarity of bark beetle communities separated the conifer species into two groups (Fig. 4a), one group including *P. sylvestris*, *P. strobus*, *P. abies*, *P. sitchensis* and *P. menziesii* and the other *A. alba*, *A. grandis* and *T. plicata*. These groups were consistent with those obtained from the phylogenetic tree built with the same conifers species and based on their DNA sequences of the *rbcL* (Fig. 4b). The first group of the Sørensen's analysis corresponded to the Pinoideae subfamily (Verhaeghe, 2003) and the second gathered the Abietoideae

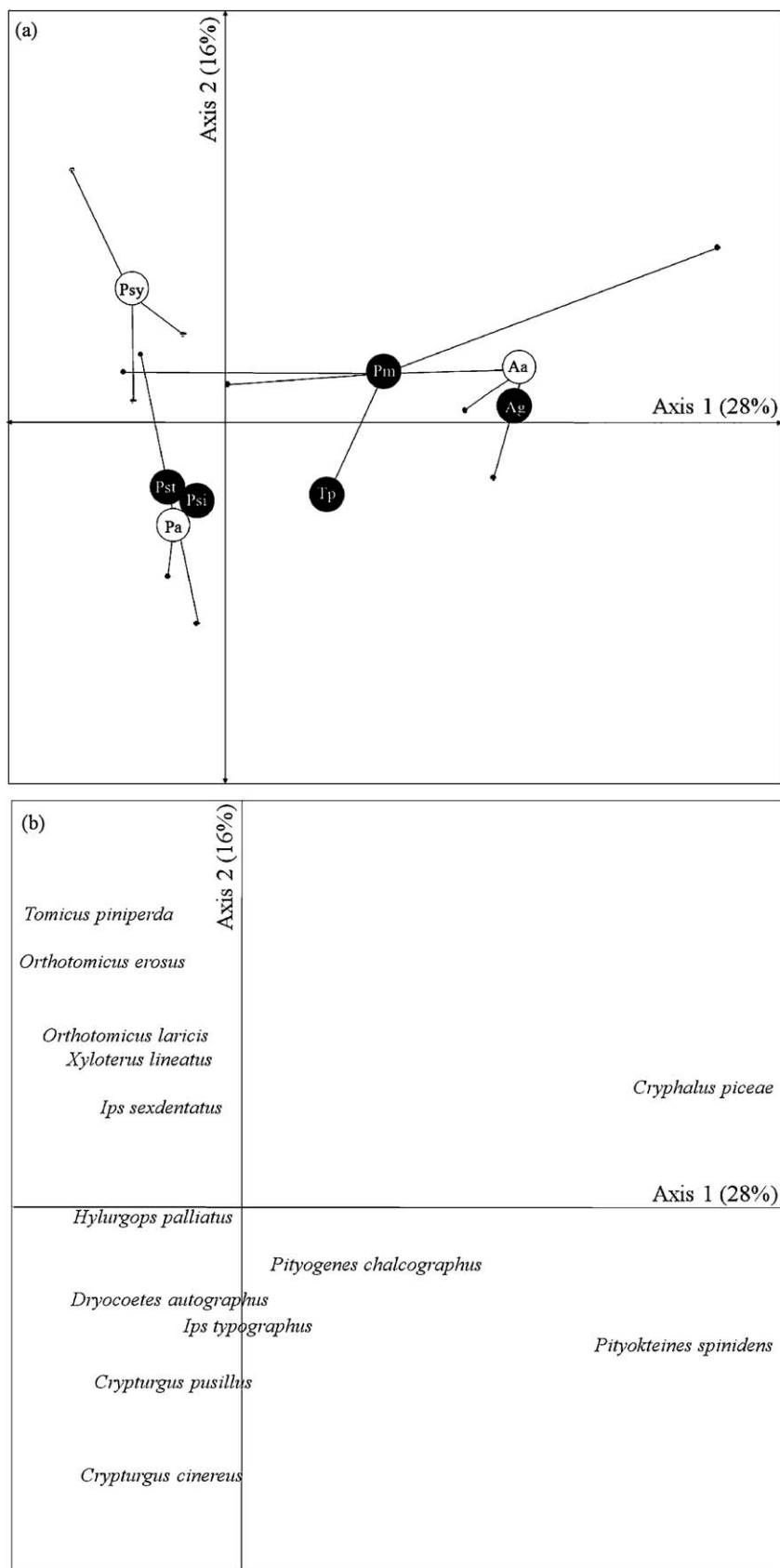


Fig. 2. (a) Factorial correspondence analysis (CoA) of the bark beetle species occurrence on different native and exotic conifer species. Projection of the sampled trees upon the axes 1 and 2 of the CoA. Points are grouped by host species identity. The white circles are placed at the gravity centre of each native host species and the black circles at the gravity centre of each exotic host species. Pa: *Picea abies*, Psi: *Picea sitchensis*, Psy: *Pinus sylvestris*, Pst: *Pinus strobus*, Aa: *Abies alba*, Ag: *Abies grandis*, Pm: *Pseudotsuga menziesii*, Tp: *Thuja plicata*. Lines indicate links between gravity centres and their corresponding samples. (b) Projection of the bark beetle species upon the plane is defined by axes 1 and 2.

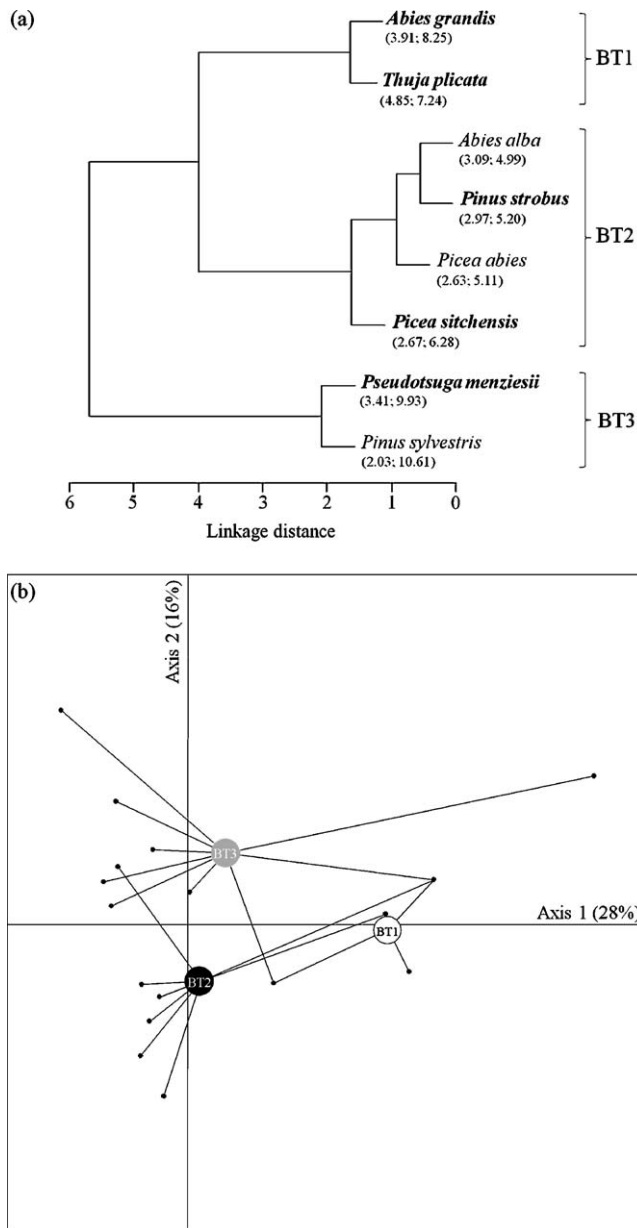


Fig. 3. (a) Clustering of native and exotic (in bold) conifer tree species on the basis of mean bark thickness similarities. Name of tree species above, in brackets, average bark thickness at 1/10th and at 9/10th of the trunk height, are indicated, respectively. (b) Factorial correspondence analysis (CoA) of the bark beetle species occurrence on different native and exotic conifer species. Projection of the sampled trees upon the axes 1 and 2 of the CoA. Points are grouped by host similarities on bark thickness. The white circle is placed at the gravity centre of conifer species belonging to the group BT1, the black circle at the gravity centre of conifer species belonging to the group BT2 and the grey circle at the gravity centre of conifer species belonging to the group BT3. Lines indicate links between gravity centres and their corresponding samples.

subfamily and the Cupressaceae family. Within each subfamily however, tree species separation according to Sørensen's quotient of similarity did not match with the phylogenetic relatedness since the two species of *Picea* and *Pinus* were not gathered together and *Abies* was closer to *Thuja* than to Pinaceae species.

3.4. Effect of the bark beetle host range

The percentage of exotic tree species colonised by each beetle species was positively and significantly correlated with the

percentage of native tree species colonised (Pearson's coefficient $r = 0.67$, $P = 0.01$, $n = 13$; Fig. 5).

4. Discussion

4.1. Bark beetles diversity

Eighteen of the 60 indigenous bark beetle species reported on conifers in France (Balachowsky, 1949) were collected. Many species were missing, probably because we only investigated eight conifer species in two regions and focused on the bole on freshly felled trees only, but our sampling included 12 beetle species considered as important pests in Europe (Grégoire and Evans, 2004). The beetles' host range observed in our study is congruent with previous field reports (Balachowsky, 1949; Chararas, 1962). Most bark beetle species were collected on their preferred host species or genus or tree species already known to belong to their host range. *H. cunicularius*, *I. acuminatus*, *P. curvidens*, *P. pityographus*, and *X. saxesenii* were however rare in our study although they are generally described as common on the investigated conifer species. *Ips sexdentatus* and *P. chalcographus* were reported for the first time on *P. menziesii* and *T. plicata*, respectively.

4.2. Exotic conifer species were not more attacked than natives ones

Although the exotic conifer species considered here were introduced in France less than 200 years ago (Riou-Nivert, 1996), they were all colonised by indigenous bark beetle species. We found no significant difference when comparing the cumulated species richness according to the tree status (native or exotic). This suggests that the potential rate of recruitment of the exotic species is at least equal to that of the native ones. Surprisingly, the introduced North American bark beetle species *G. materiarius* was not more present on its native hosts (various Pinaceae genera, Balachowsky, 1949) than on the European Pinaceae species, while *X. germanus* showed a good ability to colonise new hosts. The CoA identified two significantly distinct communities of indigenous bark beetles according to the native or exotic status of their host trees. Consequently, the native or exotic status of host trees may have a certain influence on colonisation by bark beetles. The analyses of other factors such as species host identity and bark thickness should bring to light the distribution modalities of bark beetle assemblages.

4.3. Importance of the host tree identity and their taxonomic relatedness

Many bark beetle species are known to have a wide potential host range within the Pinaceae family, but their attacks are generally concentrated on one genus: *Pinus* for *T. piniperda*, *Abies* for *C. piceae* or *Picea* for *I. typographus*, (Balachowsky, 1949; Chararas, 1962). Furthermore, host selection experiments show they exhibit a certain preference towards their main hosts (Gratton and Welter, 1998; Bertheau et al., in press). It is thus not surprising that host tree species played a fundamental role in structuring bark beetle communities in our study. It was confirmed by the CoA, which grouped the exotic *P. sitchensis* and *A. grandis* with their respective native congeners. This supported the observation that beetles tend to specialise on a particular genus. Similar groupings have also been reported when considering larval performances of *Dendrolimus sibiricus* Tschtv. on different native and introduced European conifers during quarantine experiments in Belgium (Kirichenko et al., 2008). However, both in our study and in Kirichenko et al. (2008), *P. strobus* was associated with *Picea* rather than with *P. sylvestris*. Apart from this exception, our results supported the hypothesis that the presence of closely related

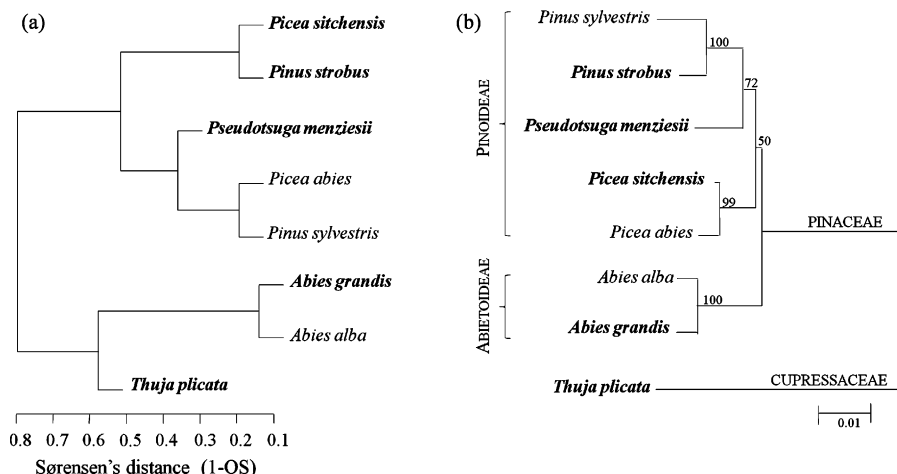


Fig. 4. (a) Similarity of bark beetle species communities between conifer tree species based on the Sørensen's quotient of similarity. (b) Phylogenetic reconstruction of the studied conifer species obtained by Neighbor Joining analysis of nucleotide sequences of *rbcL*-gene. Number indicated bootstrap support based on 100 replicates, $P < 0.05$. Exotic tree species are in bold.

native host plants in the area of introduction increases the likelihood that exotic plants will be colonised by indigenous insects (Connor et al., 1980; Strong et al., 1984). The results from the Sørensen's index of similarity comparing bark beetle communities among the different conifer species also support this hypothesis since the two main groups obtained with this analysis matched with the two subfamilies Pinoideae and Abietoideae. However, within the subfamily Pinoideae, the grouping of the tree species was not congruent with their phylogenetic relatedness. The similarity among beetle communities was indeed lower between congeners (*P. sitchensis* vs. *P. abies* and *P. strobus* vs. *P. sylvestris*) than between non-congeners (*P. sylvestris* vs. *P. abies* and *P. menziesii* vs. *P. sylvestris* or *P. abies*). Our results thus support the idea that tree taxonomic relatedness is an important factor favouring host shift, but only at the subfamily level.

4.4. Influence of the resource similarities

Host range and host specificity can be related to plant relatedness since insect communities can reflect phylogenetic distance between their host plants (Ødegaard et al., 2005). The relationship between insect recruitment and host-plant taxonomy often results from chemical and/or morphological similarities

among related plant species (Ehrlich and Raven, 1964; Connor et al., 1980; Strong et al., 1984), suggesting that these similarities can be more decisive than the phylogenetic relationships *per se* (Ehrlich and Raven, 1964; Hatcher, 1994; Becerra, 1997; Wahlberg, 2001). Indeed, it is not uncommon to find two unrelated species sharing similar resources, although this is more frequent among closely related species. In general, bark thickness is a good segregating factor among sympatric bark beetle species (Paine et al., 1981; Amezaga and Rodríguez, 1998) as well as among different hosts for a given bark beetle species (Bertheau et al., in press). In the present study, three different groups of conifers were observed according to similarities in their bark thickness, each group being associated with particular bark beetle communities, according to the CoA. Some beetle species established on trees showing a heterogeneous and thick bark such as *P. sylvestris* or *P. menziesii*, whereas others selected trees having a homogeneous and thin bark such as *P. abies* or *P. strobus*. A similar bark thickness in native and exotic tree species could therefore facilitate the indigenous bark beetles' shift. This would explain the grouping of *P. strobus* with *Picea* instead of *P. sylvestris* in the CoA or using the Sørensen's distances. Some bark beetle species seem thus to seek similar resources (e.g. thin bark) rather than phylogenetic relationships, as previously stated (Bertheau et al., in press).

4.5. Other host-related influencing factors

Abundance of both exotic and native tree species could also affect the likelihood of beetles' host shift. The larger the resources represented by introduced plants are, the more rapidly the insects can adapt to these new hosts (Strong, 1974; Strong et al., 1977; Degomez and Wagner, 2001). Together with bark thickness similarities with *P. sylvestris*, this could also explain why *P. menziesii*, the most planted conifer species in France (Riou-Nivert, 1996), exhibited high bark beetle species richness although it has no congener in Europe. Furthermore, a close geographical proximity of widespread and abundant native hosts could also help the shifting of indigenous insects to even unrelated exotic hosts (Winter, 1974; Strong et al., 1984). Pinaceae are well represented in France and are the most planted conifer species, particularly in Limousin and Jura (Riou-Nivert, 1996). In these two regions, native Pinaceae species, mainly *P. abies* and *P. sylvestris*, dominate coniferous forests and all plots of exotic species were within a distance of 500 m from a native species. A rich regional pool of indigenous bark beetle species was thus available to

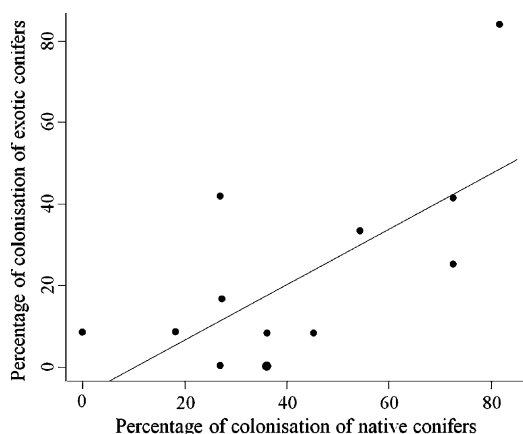


Fig. 5. Correlation between the percentage of colonised exotic conifers and the percentage of colonised native conifers (one dot corresponds to one bark beetle species and the larger dot to two bark beetle species). Pearson's coefficient correlation: $r = 0.67$, $P = 0.01$.

colonise exotic Pinaceae species. Nonetheless, a further study would be necessary to state the influence of plantation surface on beetle colonisation likelihood.

4.6. Influence of the insect host specificity

Polyphagous species tend to be better colonisers of exotic trees than specialists (Strong et al., 1984; Fraser and Lawton, 1994) and thus, if plant- and stand-related factors influence the colonisation process of bark beetles, they must be considered in relation to insect host specificity. Our results show that indigenous beetles having a wide host range, such as *P. chalcographus*, *I. typographus*, *H. palliatus* or *D. autographus*, colonised the highest numbers of exotic conifers species. This suggests that the success of bark beetles' shift onto new host tree depends on their plasticity, i.e. on their tolerance to new diets, oviposition sites or on their capacity to cope with tree defences. *P. chalcographus* even appeared highly plastic since it was able to colonise even *T. plicata*, a genus which did not belong to the family of its ordinary host range.

Compared to most phytophagous insects, bark beetles develop entirely and during almost their whole life cycle inside their host plants and are thus intimately linked to them. Consequently, they are expected to exhibit more difficulties for shifting and to need more time to adapt to novel hosts than other phytophagous species (Strong et al., 1984; Gaston et al., 1992; Lieutier, 2006). In our study, bark beetles exhibited a rather good ability to adapt to exotic species, at least among the Pinaceae family since only one non-Pinaceae species was considered. Future studies involving a larger tree range and including more unrelated tree species would allow a better understanding of the effect of bark beetle host specificity and plasticity.

5. Conclusions

Our results support the assertions that indigenous phytophagous insects adapted rapidly to conifers introduced in Europe (Evans, 1987; Lindelöw and Björkman, 2001; Dalin and Björkman, 2006; Lieutier, 2006; Roques et al., 2006). The shift of indigenous bark beetle species on exotic host trees appeared to be driven by the cumulated effects of different factors more or less correlated with each other. The presence of phylogenetically related native conifers species and that of similar resources seemed to play a decisive role, in combination with insect host specificity. But further factors like the abundance of host tree species and the geographical proximity of native tree species around the exotic ones might also be involved. Tree taxonomic proximity appeared to be a good predictor of shifting probability and the simplest one to consider in forest management, for risk assessment of indigenous bark beetle attacks on newly introduced conifers. Planting exotic trees within stands of taxonomically unrelated species might reduce the rate of bark beetle adaptation to the novel hosts. Despite the forecasts performed by previous studies (Zobel et al., 1987; Dalin and Björkman, 2006), our inventory showed that nowadays exotic conifers in France are as colonised by indigenous bark beetles as native ones. However and as pointed out by (Degomez and Wagner, 2001), from a purely economic perspective, the total number of pest species on an exotic tree may be less relevant to damage than the impact of a particular pest. Among the 13 bark beetle species collected on the exotic tree species that we considered, 12 were significant conifer pests in Europe, such as *P. chalcographus* or *I. typographus* which exhibited a high ability to colonise all exotic Pinaceae species. Considering that beetle plasticity favours host shift, this last observation suggests that these two species could have a high invasive potential if introduced in exotic areas.

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