

**Einfluss von Baum- und Landschaftstrukturen  
auf xylobionte Käfer an Eichen (Coleoptera)**

- Habitateignung, Gemeinschaftsstruktur und Diversität –

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## Beiträge

Die folgende Tabelle stellt die Beiträge der jeweiligen Autoren für die dieser Arbeit zugrunde liegenden Zeitschriftenartikel dar. Dabei setzen sich die verwendeten Kürzel aus den Anfangsbuchstaben der Autoren zusammen. Die Autoren sind gemäß ihres Arbeitsanteils an den Entstehungsschritten der Artikel angeordnet.

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## Einleitung und Zusammenfassung

### **Einleitung**

Menschen beeinflussen und verändern das natürliche Landschaftsbild in Europa seit langer Zeit (Peterken 1981, Kirby & Watkins 1998, Mitchell 2005). Diese Prozesse wirken sich vor allem auf die Qualität von Habitaten und deren Verteilung im Raum aus und können damit eine existenzielle Bedeutung für einzelne Arten oder Artengruppen haben. Letztendlich haben menschliche Eingriffe in natürliche Prozesse eine Dynamik entwickelt, die von einem rasanten Rückgang der weltweiten Artenvielfalt gekennzeichnet ist (Singh 2002). Die Bedeutung von Biodiversität für Ökosysteme war lange Zeit relativ unerforscht. Forschungsergebnisse in den letzten 20 Jahren verdeutlichen aber die Bedeutung von Biodiversität für das Funktionieren von Ökosystemen und für die Bereitstellung bestimmter Ökosystemleistungen (vgl. Hooper et al. 2005, Lyons et al. 2005).

Der Rückgang der Artenvielfalt wurde bereits 1992 im UN-Übereinkommen über die biologische Vielfalt als Problem erkannt. Auch 10 Jahre danach trat jedoch keine messbare Verbesserung der Lage ein. Die Weltgemeinschaft beschloss daraufhin auf dem Gipfel in Johannesburg 2002 das Ziel einer signifikanten Reduktion des Verlustes an Arten bis 2010. Europäische Lösungsansätze gehen sogar noch weiter und erklären eine Eindämmung des Verlustes der Artenvielfalt bis 2010 als Ziel (Kommission der Europäischen Gemeinschaften 2001). Darin wird ein Schutz der für Europa wichtigsten Habitate und Arten ebenso gefordert wie der allgemeine Schutz von Biodiversität und von Ökosystemen inklusive deren Leistungen. Auch eine Stärkung der Wissensbasis für Naturschutz und Nachhaltige Nutzung wird für eine Strategie gegen den Verlust der Artenvielfalt als wichtig erachtet (Kommission der Europäischen Gemeinschaften 2001). Gerade angewandte Studien zu Faktoren, die die Artenvielfalt beeinflussen, gewinnen dabei an Bedeutung. Eine wichtige Artengruppe, die von anthropogenen Landschaftsveränderungen betroffen ist, sind xylobionte (=holzbewohnende) Käfer. Sie sind mitverantwortlich für die Zersetzung von Holzmaterial und spielen daher eine bedeutende Rolle bei der Remineralisierung organischer Substanz (Speight 1989, Grove 2002). Sie kennzeichnen sich durch eine hohe Zahl spezialisierter und bedrohter Arten, sowie einen allgemeinen Artenreichtum verglichen mit anderen ökologischen Gruppen (vgl. Palm 1959, Haase et al. 1998, Alexander 2003). Xylobionte Käfer eignen sich damit als Modellgruppe

für Untersuchungen zur Artenvielfalt und zu den Auswirkungen von Habitatveränderungen.

Durch menschliche Aktivität bedingte Veränderungen in den Lebensräumen von Arten müssen sich nicht zwangsläufig als negativ erweisen. Einige historische Landnutzungsformen und deren Ergebnisse in der Landschaftsstruktur und im Landschaftsbild, z.B. Hudewälder, ermöglichten das räumliche Nebeneinander verschiedener Tier- und Pflanzenarten mit den unterschiedlichsten Ansprüchen an ihre Umwelt (vgl. Peterken 1981, Pott & Hüppe 1991, Falke et al. 2000). Mit der Aufgabe dieser historischen Nutzungsformen veränderten sich die Umweltbedingungen in diesen Gebieten, so dass für einzelne Arten daraus existenzielle Bedrohungen entstanden und somit in weiten Regionen Mitteleuropas auch aufgrund der Fragmentierung der Resthabitate ein Prozess des Aussterbens begann (vgl. zu den Auswirkungen von Fragmentierung Saunders et al. 1991).



**Abb. 1** Untersuchungsgebiete in Deutschland (Beiträge I-III). 1 – Gartower Elbmarsch Niedersachsen), 2 – Mittlere Elbe bei Dessau.

Beide Gebiete sind Teil des Biosphärenreservates Flusslandschaft Elbe.

## **Der Eichenheldbock *Cerambyx cerdo* als Modellart**

Besonders alt- und totholzgeprägte Biotope sind seither sehr selten in der mitteleuropäischen Kulturlandschaft geworden. Diese beherbergen aufgrund ihres Reichtums an Strukturen und Mikrohabitaten eine große Artenvielfalt an Insektenarten. Es verwundert also nicht, dass über 60% der xylobionten Käferarten als mindestens gefährdet für den deutschen Raum eingestuft werden (Geiser 1998). Nur wenige xylobionte Käferarten (z.B. *Osmoderma eremita* und *Cerambyx cerdo*) erhielten durch die FFH-Richtlinie einen europaweiten Schutzstatus, da starke Bestandsrückgänge und lokales Aussterben über den gesamten europäischen Raum beobachtet wurden. Dabei verwundert im Fall des Heldbocks (*Cerambyx cerdo*), wie sich ein noch am Anfang des 20. Jahrhunderts als verbreiteter Forstschädling (vgl. Escherich 1923, Rudnew 1936) eingestuftes Insekt im Laufe von weniger als 100 Jahren zu einer vom großflächigen Aussterben bedrohten Art entwickeln konnte. Diesen Prozess in seinen Ursachen zu erforschen und eine Trendumkehr dieses Prozesses herbeizuführen, ist für den Naturschutz auch in Deutschland eine prioritäre Aufgabe. Wichtige bekannte Ursachen für den Rückgang der Bestandesgrößen und der Zahl der Populationsnachweise sind in der Bindung von *Cerambyx cerdo* an Alteichenbäume und das Verschwinden dieser Strukturen in der heutigen Kulturlandschaft zu finden (vgl. Neumann 1985). Die Art ist in Deutschland ausschließlich an Stiel- und Traubeneichen gebunden (Müller 2001). Dabei befällt er als Starkholzspezialist in der Regel erst Stämme von einem Durchmesser größer als 80 cm (Neumann 1985, Zuppke 1993). Diese Stämme sollten idealerweise besonnt und arm an Unterwuchs sein. Solitär stehende Eichen bzw. stark belichtete Wälder und Waldränder mit Alteichenbeständen erfüllen diese Bedingungen und werden als Brutbäume von *Cerambyx cerdo* benutzt (Rudnew 1936; Neumann 1985). Auch alte Hudewälder entsprechen sekundär den Habitatanforderungen des Großen Eichenheldbockes (vgl. Müller 2001).

Ich habe mich beispielhaft mit dem Eichenheldbock *Cerambyx cerdo*, hinsichtlich seiner Habitatanforderungen und Rolle in der an Eichen lebenden Gemeinschaft xylobionter Käfer beschäftigt (Beiträge I und II).



## **Einfluss des Landschaftsmanagements auf die xylobionte Gemeinschaft**

Neben der Analyse von Faktoren, die die Verteilung einzelner Arten im Raum erklären können, habe ich Parameter untersucht, die einen Einfluss auf den Artenreichtum und die Zusammensetzung der Gemeinschaft holzbewohnender Käfer haben können. Die Habitatqualität und die Habitatfragmentierung gehören dabei zu den wichtigsten Einflussfaktoren, die die räumliche Verteilung und die Populationsdynamik einzelner Arten beeinflussen (Saunders et al. 1991, Andrén 1999, Hunter 2002). Fragmentierungseffekte lassen sich auf zwei Ursachen zurückführen: Habitatverlust und Fragmentierung im engeren Sinn (Andrén 1994). In theoretischen Modellen wird Fragmentierung meist als räumliches Problem, das zum Beispiel den Individuenaustausch zwischen besiedelten Patches beeinflusst (Murell & Law 2000), wahrgenommen. Theoretische Modelle haben meist nur eine zu untersuchende Art als Grundlage, können aber für bestimmte Fragestellungen, z.B. Variabilität der Populationsgröße bedrohter Arten (z.B. Kramer-Schadt et al. 2005), einen wertvollen Erkenntnisgewinn bringen. Empirische Studien zeigen hingegen, dass Fragmentierung auch die Qualität von Habitaten beeinflusst und sich somit auf die Überlebensfähigkeit von Arten in fragmentierten Lebensräumen auswirkt (Harrison & Bruna 1999). Nur wenige Arbeiten analysieren den Einfluss von Habitat- und Fragmentierungsparametern zusammen (z.B. Thomas et al. 2001). Bei Individuen-basierten räumlich expliziten Modellen wird mittlerweile versucht, die Habitatqualität als kategoriale Variable (gute, mittlere, schlechte Qualität) mit einfließen zu lassen. Verglichen mit Fragmentierungsparametern scheinen die Habitatqualität und –fläche ungleich wichtiger zu sein (vgl. Wiegand et al. 2005).

Bei empirischen Arbeiten zur Fragmentierung von Habitaten wurden vorwiegend einzelne Arten analysiert. Studien zu den Auswirkungen von Fragmentierung auf Gemeinschaftsebene fehlen jedoch weitestgehend. Der Einfluss von Fragmentierung auf Populationen wird meist als negativ beurteilt, z.B. durch ein allgemein erhöhtes Aussterberisiko in fragmentierten Habitaten (Debinsky & Holt 2000, Stephens et al. 2004). Die Habitatkonfiguration, insbesondere deren strukturelle Diversität, ist mit der Artenzahl in Invertebratengemeinschaften positiv assoziiert (Økland et al. 1996, Siemann et al. 1998). Arthropodengemeinschaften reagieren offensichtlich relativ schnell auf Fragmentierungsprozesse (Didham et al. 1998), da sie einen kurzen Lebenszyklus haben und oft eine begrenzte Ausbreitungsfähigkeit zeigen. Bestimmte

artspezifische oder gruppenspezifische Eigenschaften sind verantwortlich für die unterschiedliche Sensibilität von Arten gegenüber Fragmentierung (Driscoll & Weir 2005).

Sowohl für den Naturschutz als auch für die ökologische Modellbildung ist es von Interesse, den Einfluss von Habitatqualität und –fragmentierung auf ökologische Gemeinschaften sowie deren mögliche Interaktionen zu verstehen. Deswegen habe ich die Gemeinschaft der an Eichen lebenden xylobionten Käfer hinsichtlich des Einflusses von Fragmentierung, Habitatqualität und Waldmanagement auf die Zusammensetzung und Artenvielfalt untersucht (Beiträge III und IV).

Die vorliegende kumulative Dissertation besteht aus vier Studien zu den beiden Themenkomplexen, die im Folgenden zusammenfassend dargestellt werden:

### **Zusammenfassung der einzelnen Beiträge**

#### ***Beitrag I: Habitatansprüche von *Cerambyx cerdo* (Cerambycidae) – eine Modellstudie für xylobionte Insekten***

Xylobionte Insekten sind bekannt für ihren außerordentlich hohen Artenreichtum und beherbergen eine hohe Zahl vom Aussterben bedrohter Arten (Speight 1989). Oft sind die Ansprüche xylobionter Arten an ihr Habitat völlig unbekannt. Eine Möglichkeit, diese Bedingungen zu studieren, stellt die Habitateignungsmodellierung dar, die auch für andere Tiergruppen, z.B. Laufkäfer (Bonn und Schröder 2001, Matern et al. 2007) oder Vögel (Schwab et al. 2006) erfolgreich eingesetzt wurde. Bisher gab es keine Untersuchungen, die dieses statistische Verfahren für xylobionte Insekten genutzt hat. Um aber einen wissenschaftlich basierten Artenschutz und geeignete Habitatmanagementmaßnahmen für solche Arten zu etablieren, sollte die Anwendbarkeit solcher Verfahren modellhaft getestet werden. Diese Untersuchung beschäftigt sich daher beispielhaft mit den Habitatanforderungen des vom Aussterben bedrohten Bockkäfers *Cerambyx cerdo*.

Im Rahmen der statistischen Modellierung wurden Datensätze aus Mitteleuropa untersucht, um die Beziehungen der Art zu ihrer Umwelt nachvollziehen zu können

und um die Variablen zu identifizieren, welche für die Habitatwahl von Bedeutung sind. Die Ergebnisse zeigen, dass die Parameter Besonnungssituation, das Vorhandensein von Saftflussstellen, die Rindentiefe und die Distanz zum nächsten besiedelten Baum geeignet sind, die Vorkommen von *C. cerdo* relativ gut vorherzusagen. Das erstellte Modell wurde räumlich validiert und bestätigte die gute Vorhersagekraft auch an einem unabhängigen Datensatz. Allgemein konnte gezeigt werden, dass baumbezogene Parameter einen stärkeren Effekt auf die Vorkommenswahrscheinlichkeit hatten als Parameter auf Landschaftsebene.

Aus diesen Ergebnissen lassen sich folgende Empfehlungen für das Management besiedelter, aber auch noch unbesiedelter Flächen ableiten. Generell ist es wichtig, großflächig die Bedingungen an den Bäumen hinsichtlich einer verbesserten Besonnungssituation der Stämme zu entwickeln. Dafür bietet sich das Konzept der halboffenen Weidelandschaft an, das auch für andere Tier- und Pflanzengruppen einen hohen Nutzen hat (Falke et al. 2000, Poschlod et al. 2002, Mountford und Peterken 2003). Für *C. cerdo* ist das Angebot geeigneter Habitate über einen längeren Zeitraum sehr wichtig, da die Art einen relativ langen Entwicklungszyklus durchlebt und nur ältere Bäume für eine Besiedlung in Frage kommen.

Dieser Beitrag kann somit zur Verbesserung des biologischen Wissens einer europaweit geschützten Art beitragen. Der Erfolg des NATURA 2000 Netzwerkes hängt auch von der Verfügbarkeit artspezifischer Daten, z.B. Ausbreitungsfähigkeit oder eben Habitatanforderungen, ab. Habitateignungsmodelle können auch für den Schutz xylobionter Insekten einen wertvollen Beitrag leisten.

### **Beitrag II: Der Eichenheldbock als Ökosystementwickler**

Seit Mitte der 1990er Jahre diskutieren Ökologen das Konzept des „Ecosystem Engineering“, d.h. den Einfluss von Organismen, die durch ihre Anwesenheit die physikalischen Bedingungen ihrer Umwelt verändern und dadurch andere Arten beeinflussen (Jones et al. 1994, Wright und Jones 2006, Byers et al. 2006, Hastings et al. 2007). Insbesondere in der Naturschutzbiologie ist die funktionale Rolle von Organismen von Interesse, weil es ganze Gemeinschaften auch bedrohter Arten gibt, die von einzelnen Arten abhängig sind (z.B. Pintor und Soluk 2006).

Der Große Eichenheldbock (*Cerambyx cerdo*) hat in den letzten hundert Jahren einen dramatischen Rückgang der Zahl der Populationen und der Populationsgrößen

erfahren (Klausnitzer et al. 2003). Die Art ist deswegen auch in der FFH-Richtlinie als bedrohte Art eingestuft (Council of the European Communities 1992).

Die Tätigkeit von *C. cerdo*-Larven in vor der Besiedlung vitalen Eichenbäumen verändert deutlich physikalisch messbare Eigenschaften dieser Bäume. Diese Untersuchung analysiert die Auswirkungen dieser Veränderungen auf den Artenreichtum und die Struktur der an Eichen lebenden xylobionten Käfergemeinschaft. Dabei werden Fänge aus Luftklebnetzen an 10 vom Eichenheldbock besiedelten Eichen mit solchen von 10 von ihm unbesiedelten Eichen verglichen. Die Untersuchung wurde im Biosphärenreservat Niedersächsische Elbtalaue durchgeführt.

Von *C. cerdo* besiedelte Eichen hatten dabei eine artenreichere Gemeinschaft als vergleichbare unbesiedelte Eichen. Die physikalisch durch den Eichenheldbock veränderten Bäume beheimateten auch deutlich mehr bedrohte Käferarten. Die Studien dieses Beitrages zeigen, dass eine bedrohte Käferart das eigene Habitat dahingehend verändern kann, dass andere bedrohte Arten bessere Habitatbedingungen vorfinden. Damit hätten Schutzmaßnahmen für *C. cerdo* auch einen positiven Effekt für die gesamte xylobionte Gemeinschaft, insbesondere für einige stark bedrohte Arten. Diese Ergebnisse sprechen für eine Wiederansiedlung des Eichenheldbockes in Gebieten, wo die Art bereits ausgestorben ist. Zumindest sollten aber die Bedingungen in noch bestehenden Populationen von *C. cerdo* verbessert bzw. angrenzende Bereiche entsprechend gemanagt werden.

### ***Beitrag III: Einfluss von Fragmentierung und Habitatqualität auf die Struktur und Zusammensetzung der xylobionten Gemeinschaft an Eichen***

Habitatqualität und Habitatfragmentierung gehören zu den wichtigsten Faktoren, die die räumliche Verteilung von Pflanzen- und Tierarten beeinflussen. Deswegen spielen diese beiden Faktoren auch eine Rolle bei der Populationsdynamik einzelner Arten und wirken sich auch auf die Struktur, Zusammensetzung und den Artenreichtum von Gemeinschaften aus (Saunders et al. 1991, Hunter 2002). Theoretische Modellansätze diskutieren Fragmentierung als ein räumliches Problem, das den Individuenaustausch zwischen einzelnen Habitaten und die Populationsgröße beeinflusst. Dagegen zeigen empirische Studien, dass Habitatfragmentierung sich auch auf die Habitatqualität selbst auswirkt (Harrison und Bruna 1999). Bisher haben nur wenige Studien beide Aspekte zusammen untersucht

(z.B. Thomas et al. 2001). Insbesondere fehlen Arbeiten, die sich mit den Auswirkungen von Fragmentierung und der Interaktion mit der Habitatqualität in artenreichen Gemeinschaften beschäftigen. Deswegen wurde für diese Studie die artenreiche Gruppe der xylobionten Käfer untersucht, um einen Einblick in die Gemeinschaftsstruktur und den Artenreichtum unter dem Einfluss von Fragmentierung und wechselnden Habitatqualitäten zu gewinnen. Die Fragestellung wurde an 28 Eichen bearbeitet, die entweder solitär oder im Verbund stehen.

Die quantitative Analyse der Faktoren, die den Artenreichtum beeinflussen, ergab, dass Habitatparameter einen wesentlich größeren Teil der Varianz erklären können als Fragmentierungsparameter. Solitär stehende Eichen zeigten eine höhere Zahl xylobionter Arten als vergleichbare Bäume im Bestand. Das gilt ebenfalls für die Zahl der bedrohten Arten. Einige trophische Gruppen reagierten trotzdem relativ stark auf Fragmentierungsparameter. Insbesondere Arten, die in der Nahrungspyramide weit oben stehen, z.B. Prädatoren, scheinen von Fragmentierung besonders betroffen zu sein. Es ist allgemein bekannt, dass die Artenzahl einer Fläche mit steigender Flächengröße zunimmt (Cockburn 1995). Die „trophic rank hypothesis“ (Holt et al. 1999) besagt, dass davon nicht alle trophischen Ebenen in einer Gemeinschaft gleich stark betroffen sind. Dabei wird erwartet, dass Arten oder Gruppen auf höherer trophischer Ebene einen stärkeren Zusammenhang zwischen Artenzahl und Flächengröße oder anderen Fragmentierungsparametern zeigen. Diese Arten haben für gewöhnlich relativ niedrige Populationsgrößen oder eine niedrige Abundanz und sind deswegen mehr anfällig für lokale Aussterbeereignisse (Henle et al. 2004). Angewandt auf die untersuchten Eichen bedeutet dies, dass Solitäreichen (geringe Flächengröße) größere Populationen von räuberischen Käfern nicht beherbergen können. Aufgrund der Isolation von anderen Bäumen sind Solitäreichen für Arten mit einer niedrigen Populationsgröße statistisch gesehen auch schlechter erreichbar.

Die Isolation von Eichen ist auch für veränderte Habitatbedingungen für xylobionte Käfer an den Solitäreichen verantwortlich. Einzelne stehende Eichen haben verglichen mit Waldeichen andere Mikroklimata und Mikrohabitate. Daraus lässt sich folgern, dass sowohl Solitäreichen als auch Waldbäume für den Schutz der Gesamtheit der xylobionten Käferfauna notwendig sind. Schutzmaßnahmen sollten darauf gerichtet sein, zumindest einzelne Waldbereiche hin zu halboffenen Beständen zu entwickeln. Weiterhin empfiehlt sich das Anpflanzen von einzeln stehenden Eichen, um auch in

den nächsten Jahrhunderten noch geeignete Habitate für spezialisierte Arten zur Verfügung zu haben.

***Beitrag IV: Strukturelle Unterschiede in drei verschieden genutzten mediterranen Wäldern und deren Auswirkungen auf die xylobionte Käferfauna***

Die Mediterraneis ist sowohl für Pflanzen- als auch für Tierarten ein Zentrum der Biodiversität (Médail und Quézel 1999, Myers et al. 2000). Eichenwälder gehören in den Ländern mit einem mediterranen Klima zur natürlichen Vegetation, sind aber oft von einer Jahrtausende alten Übernutzung durch Brennholzgewinnung und Waldweide geprägt (Maranón et al. 1999, Grove und Rackham 2003). Heute noch bestehende Waldstandorte sind auf verschiedene Art und Weise genutzt worden oder werden heute noch so bewirtschaftet. Diese unterschiedlichen Wirtschaftsweisen wirken sich in aller Regel auf die Baum- und Waldstruktur mit einem unterschiedlichen Angebot an Habitaten für totholzbewohnende Organismen aus.

Im Rahmen dieser Arbeit wurden drei verschieden genutzte Waldstandorte in Israel untersucht. Dabei wurde die Qualität und Quantität der Totholzstrukturen kartiert sowie deren Auswirkungen auf die xylobionte Käferfauna analysiert. Die Ergebnisse zeigen signifikante Unterschiede im Durchmesser der Bäume, der Anzahl der Stämme pro Flächeneinheit und der Vielfalt der Totholzstrukturen zwischen den drei Standorten. Halboffen stehende Alteichen zeichneten sich durch die größte Vielfalt an Totholzstrukturen aus und brachten die meisten xylobionten Arten sowie die meisten Individuen hervor. Die höchste Artenzahl nach Rarefaction fand sich allerdings auf dem durch Schneitelung der Bäume geprägten Waldstandort. Dort konnte eine relativ hohe Stammdichte an mittelalten Eichenbäumen kartiert werden. Die Zahl der xylobionten Käferarten war stark mit dem Durchmesser also mit dem Alter der Bäume korreliert.

Diese Ergebnisse zeigen, dass alte Baumindividuen auch in mediterranen Waldlandschaften eine wichtige Funktion für die Erhaltung der Artenvielfalt xylobionter Insekten innehaben. Die unterschiedlichen Methoden der Waldnutzung werden in für die xylobionte Gemeinschaft wichtigen strukturellen Parametern reflektiert. Die mediterranen Waldlandschaften im Nahen Osten stellen eine wichtige

Ressource der Insektenvielfalt in dieser Region dar. Von besonderer Bedeutung sind dabei nachhaltig genutzte Waldstandorte, da diese eine kontinuierliche Bewaldung und damit eine relative Habitatkontinuität gewährleisten.

## **Fazit**

Mit Hilfe der durchgeführten Studien konnten ökologische Schlüsselfaktoren für die vom Aussterben bedrohte Bockkäferart *Cerambyx cerdo* identifiziert und erstmals quantifiziert werden. Diese Faktoren zeigen die enge Habitatbindung der untersuchten Art und erweitern die bisherigen Kenntnisse über die Biologie der FFH-Art. Es konnte gezeigt werden, dass dieser Bockkäfer vor allem ältere, besonnte Eichen mit Saftfluss besiedelt. Erst ein Mindestdurchmesser von 60 cm erhöht die Vorkommenswahrscheinlichkeit signifikant. Strukturell zur Besiedlung geeignete Habitats müssen sich allerdings auch in relativer räumlicher Nähe zu anderen, bereits besiedelten Bäumen befinden. Das verdeutlicht das geringe Ausbreitungspotential der Art. Erstmals untersucht zeigte sich auch, dass von *C. cerdo* besiedelte Eichen artenreicher sind als andere vergleichbare Eichen. Seine wahrscheinliche Rolle als Ökosystementwickler und der mit ihm assoziierte Artenreichtum unterstreicht seine europaweite Bedeutung für den Schutz der xylobionten Käferfauna. Das bestätigt die bisher ohne entsprechende Untersuchung seiner ökologischen Rolle getroffene Einordnung als „FFH-Art“.

Verschiedene Managementansätze zum Erhalt der Art werden diskutiert. Durch die Freistellung einzelner Bäume oder Waldbereiche in unmittelbarer Nachbarschaft zu besiedelten Eichen können bestehende Populationen gezielt gefördert werden. In Anbetracht des schwachen Ausbreitungspotentials der Art empfehlen sich auch Wiederansiedlungen in weiter entfernten Gebieten. Dabei ist zu berücksichtigen, dass es eine genügend große Anzahl von Eichen in verschiedenen Altersklassen gibt, um eine langfristige Populationsentwicklung und –etablierung zu gewährleisten. Um der Knappheit potentiell besiedelbarer Habitat in Zukunft vorzubeugen, sollten Anpflanzungen von Solitäreichen vorgenommen werden, zumal diese Bäume eine artenreiche xylobionte Gemeinschaft aufgrund ihrer speziellen Lage beherbergen. Langfristig gesehen bieten wahrscheinlich durch Beweidung gepflegte großräumige halboffene Landschaften die besten Bedingungen für den Schutz von *C. cerdo* als auch für die Erhaltung einer artenreichen xylobionten Insektenfauna.

Isolierte Solitärbäume beherbergen eine vergleichbare, z.T. sogar höhere Artenvielfalt als Bäume im geschlossenen Bestand. Die Artenvielfalt wird weitgehend von ökologischen Habitatparametern bestimmt. Fragmentierungsparameter spielen eine untergeordnete Rolle. Trotzdem findet sich an Solitärbäumen eine andere Zusammensetzung der xylobionten Fauna, wobei höhere trophische Gilden, z.B. räuberisch lebende Käfer, von einer Fragmentierung ihrer Habitate negativ beeinflusst werden. Grundsätzlich wird angenommen, dass Eigenschaften wie Flugfähigkeit, Körpergröße und Habitatbindung die Sensibilität von Arten gegenüber Fragmentierung ihrer Habitate beeinflussen. Im Rahmen dieser Arbeit konnte gezeigt werden, dass auch die Stellung innerhalb des Nahrungsnetzes der xylobionten Gemeinschaft die Sensibilität einer Art für Fragmentierung bedingt. Für tropische Waldfragmente konnte gezeigt werden, dass epigäisch lebende Räuber ebenfalls stärker von Fragmentierung betroffen sind als andere epigäisch lebende Arten (Didham et al. 1998). Bisherige Untersuchungen bei Invertebraten analysierten vorwiegend bodenbewohnende Käfer (Didham et al. 1998, Davies et al. 2000). Bei der Gemeinschaft xylobionter Käfer konnte die Rolle von Fragmentierung erstmals in dieser Arbeit analysiert werden. Die Ergebnisse unterstützen die sogenannte „Trophic rank-hypothesis“ (Holt et al. 1999), nach der vor allem Arten aus höheren trophischen Ebenen von Veränderungen der Flächengröße (und eventuell der Isolation) betroffen sind.

Solitäreichen, insbesondere alte Exemplare, haben einen hohen naturschutzfachlichen Wert für xylobionte Käfer und andere Tiergruppen, da diese Eichen sich in wichtigen physiologischen Parametern von anderen Eichen unterscheiden. In mediterranen Gebieten beherbergen alte Eichen eine Vielzahl von holzbewohnenden Käferarten. Neben Alteichen sind vom Menschen genutzte Schneitelwälder ein guter Ansatz für die Erhaltung von Biodiversität im mediterranen Raum.

Zukünftige Managementansätze sollten auf ein enges räumliches Nebeneinander von geschlossenen Beständen und Solitärbäumen zielen. Das Konzept der halboffenen Weidelandschaft bietet dafür eine mögliche Grundlage.

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**I** Modelling habitat and spatial distribution of an endangered  
longhorn beetle – A case study for saproxylic insect  
conservation

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## Abstract

Saproxylic insects are characterised by their exceptional diversity and high proportion of threatened species. No recent studies have demonstrated the validity of habitat suitability analysis for scientifically based habitat management for these species. We studied the habitat requirements of the endangered longhorn beetle *Cerambyx cerdo*, a species with a supposed keystone function for the saproxylic insect community living on oaks. We used species distribution modelling based on datasets from Central Europe to understand the species–habitat relationships and to find the environmental variables responsible for habitat selection of *C. cerdo*. Our results show that the most important parameters, insolation, presence of oak sap, bark depth and the distance from the next colonised tree, are able to predict the presence of *C. cerdo* very well. A spatial validation procedure revealed very similar predictive power, indicating the general validity of our model. Tree-level parameters were shown to have a stronger effect on the occurrence probability than landscape-level predictors. To improve the tree-level conditions (e.g. insolation on the trunk) habitat management in the form of semi-open pasture landscapes is recommended from which many other taxa will also draw considerable benefit. The provision of such conditions over decades is the essential key in the conservation of this longhorn beetle species. The success of the European network of conservation areas “Natura 2000” heavily depends on broad biological knowledge of the designated protected species. The present paper shows that species distribution models can give valuable contributions for conservation in saproxylic insects.

## 1 Introduction

Habitat models for species of conservation interest are of key importance and value in landscape planning and reserve development (Fleishman et al., 2002). Despite the large number of threatened species of wood-dependent insects there is no recent verification whether an habitat suitability analysis is useful for a scientific based habitat management in these species. We chose the longhorn beetle *Cerambyx cerdo* L. (Coleoptera, Cerambycidae) for this study on saproxylic insects because of its vulnerability and because there is considerable interest in conserving the remaining populations of this beetle throughout Europe. Saproxylic insects are defined by Speight (1989) as invertebrates ‘that are dependent, during some part of their life

cycle, upon the dead or dying wood of moribund or dead trees or upon wood-inhabiting fungi, or upon the presence of other saproxylics'. This longhorn beetle is one of the protected species explicitly named in the Habitats Directive with the goal of maintaining existing populations and establishing long-term survival (Council of the European Communities, 1992). Furthermore, the species is receiving worldwide attention through the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Many saproxylic species are affected by modern forestry and the shortage of old trees in our landscape today (Ranius and Jansson, 2000; Lindhe and Lindelöw, 2004) with the result that more than 60% of saproxylic beetle species in Central Europe are currently threatened by extinction (Geiser, 1998). Surprisingly, detailed studies have been conducted on the habitat requirements of only a few saproxylic beetles (e.g. Ranius and Nilsson, 1997 for *Osmoderma eremita*; Kolb et al., 2006 for *Ips pini*). Previous studies revealed that species distribution models can make a significant contribution to the conservation of different taxa: such as for birds (Manel et al., 1999), ground beetles (Bonn and Schröder, 2001; Matern et al., 2007) and butterflies (Binzenhöfer et al., 2005). Quantitative assessment of the contribution of the three components patch area, isolation and habitat quality to patch occupancy in insects has demonstrated the key importance of the factor habitat conditions (e.g. Dennis and Eales, 1997; Gutiérrez et al., 1999; Thomas et al., 2001; Heikkinen et al., 2005). Statistical habitat models provide a method to combine terms of isolation and patch area with simple habitat parameters into a complex model (Kuhn and Kleyer, 1999; Guisan and Thuiller, 2005). Taking into consideration that one major group which determines insect diversity in Central Europe belongs to saproxylic insects, we test this approach on a wood-dwelling species as a case study. Over the past 100 years there has been a sharp decline in the number of populations and in population sizes of *Cerambyx cerdo* (Klausnitzer et al., 2003). Changes in landscape structure as a result of altered agricultural and forest management practices have led to a decline in potential suitable habitats for this longhorn beetle species. This monophagous beetle in Central Europe only occurs on oaks which fulfill its specialised habitat requirements. Recent threats are a decrease in the number of old oak trees and oak dominated semi-open landscapes in general. The species was once widespread throughout Northern Africa and Europe wherever oaks grow, with the exception of Great



Britain (Bílý and Mehl, 1989). A recent survey of its distribution in Europe exhibits last viable populations in France, Germany, Poland and the Mediterranean region (Luce, 1997). The surveyed populations in Germany are among the last known populations in northern Central Europe. In order to create management plans and develop protected areas it is necessary to make a close analysis of the species habitat requirements. The aim of our paper is to test whether a habitat suitability model, considering patch area, isolation and habitat quality, can also be derived for saproxylic insects. With the help of spatial validation and conservation suggestions from our results we intend to extrapolate a nature conservation strategy with which to conserve the species rich community associated with *C. cerdo*.

## 2 Materials and Methods

### 2.1 Species

With a body length of up to 55 mm, *C. cerdo* is one of the largest longhorn beetles living in Europe. Larval development takes 3–5 years in oak trunks – in Central Europe mainly *Quercus robur* (Bílý and Mehl, 1989; Luce, 1997). The adult stages can be found on colonised trees from the end of May until the beginning of August. Emergence is not synchronised to specific years. Colonised trees can be identified by visible holes made by the larvae on the trunk or thick branches (Müller, 2001). These holes can persist over many years or even decades. Typical signs of recent activity are wood meal and fresh holes with red-coloured interior sides. Trees with many dead wood in the canopy, which is a result of larval feedings, are often colonised by *C. cerdo*.

### 2.2 Study areas

The study area was located in the 'Gartower Elbmarsch' (53°1'N, 11°27'E) where the last population of this species in Lower Saxony is to be found. This area covers approximately 105 km<sup>2</sup> and is strongly influenced by the Elbe river. The 'Gartower Elbmarsch' is an ancient cultural landscape with large areas widely covered by pastures interspersed with groups of trees and small woodlands. Most trees on which *C. cerdo* occurs are located in a narrow strip of pasture between the dike and the river. Another important location is a three kilometer long avenue with a mixture of oak trees of different ages on both sides. The second study area primarily used for

external validation in our test of model transferability in space is located about 150 km away in Saxony-Anhalt. This region still harbours the greatest number of oak trees colonised by *C. cerdo* in Germany and is well known for its park landscape with a huge number of solitary oaks. We examined sites around Dessau (51°50'N, 12°15'E) and in the 'Ochsenbusch' nature reserve near Diebzig. Both these study areas are part of the MAB (Man-and-Biosphere)-reserve "River landscape Elbe".

## 2.3 Environmental and species data

### 2.3.1 Sampling strategy

For sampling we applied a stratified approach concentrated within different transects (see Hirzel and Guisan, 2002). We first searched for all colonised trees in the known region in order to set the transects and then recorded all oaks within these transects. Additional samplings were made taking care to obtain a long gradient in the habitat variables. We recorded all colonised trees in our primary study area. Each tree was counted as a single case in the modelling process. In total, we have analysed 267 oak trees in the area in Lower Saxony and 144 oaks for the validation in Saxony-Anhalt.

### 2.3.2 Predictor variables

In total we investigated 10 habitat variables presented by these oaks (Table 1). Our dataset consists of predictor variables measured on different scales. Categorical independent variables were coded with indicator coding into design variables (Jongman et al., 1995; Hosmer and Lemeshow, 2000).

### 2.3.3 Tree-level

Investigations in this study were carried out on both the landscape and the tree-level (see Maurer, 2002). Following expert knowledge and literature (Neumann, 1985; Müller, 2001) we focussed on a relatively small number of potential predictor variables. Some of these are recorded in ordinal scale, because, for instance, it is impossible to measure the vitality of the trunk or tree canopy. The diameter of the oak trunk is an expression of the amount of available resources and is comparable to patch area. Besides these direct resource variables we used indirect gradients such as insolation, an expression of the heat conditions. To depict the potential insolation, we created an index based on an approximation of sunshine intensity, related to light

incidence and sun-exposed sides of the tree, according to Hill and Binford (2002). The average bark depth was calculated as an average from three measurements at different representative locations on the trunk.

#### 2.3.4 Landscape-level

At the landscape-level the isolation of trees is considered as a predictor. We therefore measured isolation of trees in terms of (i) the distance to the next uncolonised oak tree and (ii) the distance to the next recently colonised oak tree. Distance to the next colonised or uncolonised oak was transformed into log-scale ( $\log_{10}$ ), because of the large range. Finally, we recorded the position of the oak tree in the landscape, placing the tree in a category such as 'solitary' or 'avenue'.

#### 2.3.5 Response variables

As response variable we surveyed the intensity and the current state (presence/absence/old presence) of occurrence on each tree using visual indicators such as wood meal or fresh exit holes used from the imagines. Old infestations observed, due to visible old holes and larval feeding ways were not considered in the modelling process because habitat conditions possibly changed over decades; thus, considering old holes would yield biased parameters. We used the presence and absence of the species as the response, which is binary coded as 1 and 0.

### 2.4 Statistical analysis

To identify strong correlation between predictors, we investigated their correlation structure (Fielding and Haworth, 1995). Since the maximum bivariate correlation between predictors was  $r_s = 0.384$  (Spearman rank correlation), multicollinearity is negligible. The significance of interaction terms and quadratic functions of the parameters was tested before building the final model and it was found that none of them are relevant for predicting the response variable.

#### 2.4.1 Logistic regression

Binary logistic regression with backwards, stepwise variable selection is a common statistical method used in conservation biology to estimate occurrence probabilities in relation to predictors (Kleyer et al., 1999; Cowley et al., 2000). We developed two

different models. The so-called final model uses all significant predictors which are thought to have a contribution independent from the species presence. To calculate an alternative model we added the variables 'canopy vitality' and 'trunk vitality', which are biased by the species presence, on the dataset. The application of the last one will be discussed later in the paper. The significance of coefficients in the logistic regression model was assessed via the likelihood ratio test. We applied AIC (Akaike's Information Criterion, Akaike, 1974; Burnham and Anderson, 2002) as criterion in backward selection to compromise between model performance and complexity (cf. Oppel et al., 2004). Nagelkerke (1991)  $R^2_N$  was used for the evaluation of model calibration. To evaluate model discrimination, we calculated the area under a receiver operating characteristic (ROC) curve, the AUC-value (Hanley and McNeil, 1982; Fielding and Bell, 1997). In an ROC-plot, sensitivity, i.e. the proportion of correctly predicted occupied sites, is plotted against the term (1-specificity, i.e. 1 minus the proportion of correctly classified absences) for each possible threshold probability. A random prediction as well as a null model would yield an ROC-curve equivalent to the 45°-line, whereas a perfect classification would follow the y-axis ( $x = 0$ ) and  $y = 1$ . The area enclosed by this curve is called AUC (area under curve) which is 0.5 in the null model case and 1.0 if classification is perfect. We calculated AUC with a 95% confidence interval along with some threshold-dependent performance criteria such as correct classification rate and Cohen's kappa for several threshold probabilities applying a program provided by Schröder (2006). This software is used to assess model transferability by testing the significance of AUC-values after applying the model to independent test data. To estimate the total independent contribution of the single variables to the response, we ran a hierarchical partitioning procedure (MacNally, 2000). By this procedure, the variation in habitat occupancy is decomposed into independent and joint effects of different predictors (cf. Heikkinen et al., 2005). Thus, hierarchical partitioning helps to provide a deeper understanding of the importance of those predictors.

We carried out the statistical analyses with R 2.2.0 (R Core Development Team, 2005). Hierarchical partitioning was conducted using the 'hier.part'-package (version 1.0, MacNally and Walsh, 2004), and the 'Hmisc' (version 3.0-12) and 'Design' library (version 2.0-12) (provided by F. Harrell) were used for the logistic regression procedure. Response curves were plotted using the program LR-mesh provided by Rudner(2004).

**Table 1** Predictor variables measured from each of the oak trees

<i><b>Categorical predictor variables</b></i>	<i>Classes</i>	<i>df</i>	<i>Number of cases in presences</i>		<i>Number of cases in absences</i>	
Canopy vitality	0= mostly dead ; 1=partly dead; 2= vital	2	0=14; 1=39; 2=10		0=3 ; 1=16 ; 2=135	
Trunk vitality	0= dead parts without bark; 1= entire bark vital	1	0=19; 1=44		0=7 ; 1=147	
Oak sap	0=no sap locations; 1=sap location(s)	1	0=30 ; 1=33		0=137 ; 1=17	
Understorey vegetation	0=half trunk length and higher; 1=lower vegetation	1	0=12 ; 1=51		0=27 ; 1=127	
Position in landscape	0=solitary; 1=woodland edge; 2=patchy site; 3=woodland; 4=avenue	4	0=9 ; 1=7 ; 2=27 ; 3=1 ; 4=19		0=14 ; 1=12 ; 2=48 ; 3=25 ; 4=55	
<i><b>Continuous predictor variables</b></i>	<i>Units</i>		<i>Mean of presences</i>	<i>SD</i>	<i>Mean of absences</i>	<i>SD</i>
Trunk diameter (DBH <sup>a</sup> )	Measured at breast height in [m]	1	1.22	0.36	0.96	0.31
Distance uncolonised	in [log10 m+1]	1	1.02	0.37	0.87	0.29
Distance colonised	in [log10 m+1]	1	1.32	0.51	1.58	0.81
Sun index	[0=heavily shaded, no direct sun] to [12=sun from all directions]	1	8.05	3.58	5.79	3.82
Bark depth	Mean of three independent measures in [mm]	1	32.03	12.01	24.08	8.52

### 3 Results

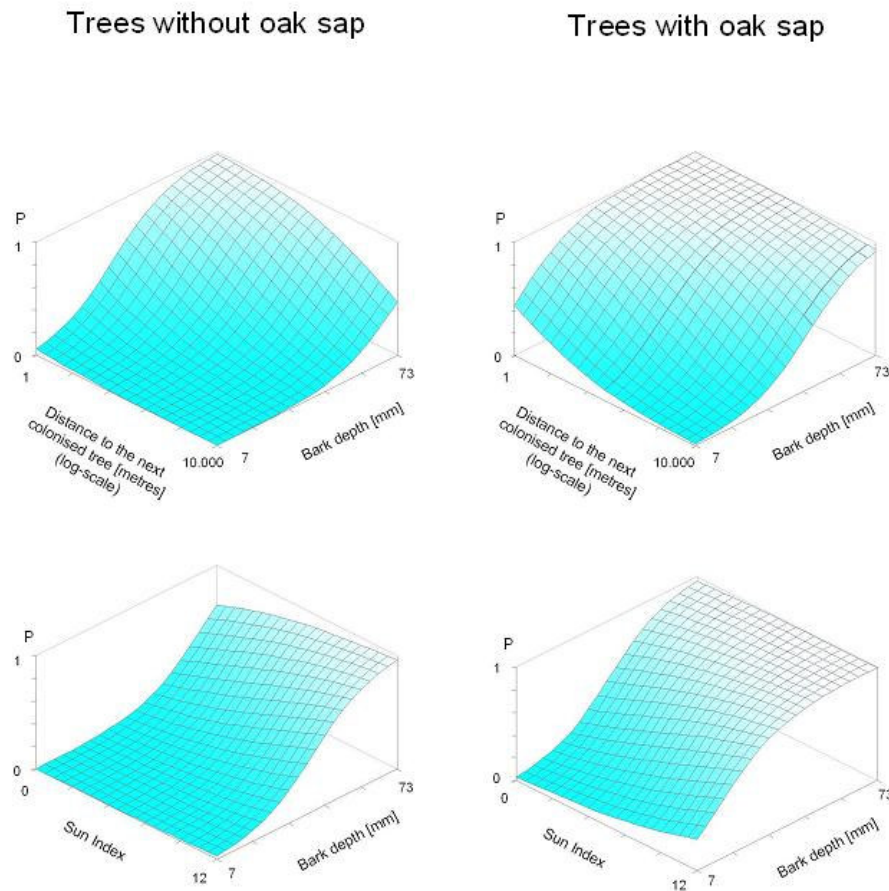
Only 62 out of 267 (24%) oaks investigated were recently colonised; 154 (58%) trees were without any characteristic signs of presence. 51 oaks (19%) were classified as old presence trees. Thus, our final sample size is  $n = 216$  trees.

#### 3.1 Habitat parameters related with species presence

The final model considers four predictors with a strong effect on the occurrence probability (see Table 2 with response surfaces shown in Fig. 1). We found that increasing bark depth, sun intensity and presence of oak sap leads to significant higher occurrence probabilities in *C. cerdo*. Increasing distance to the next colonised tree leads to weaker conditions for colonizing an oak (Fig. 1). This is the only significant landscape effect in the regression procedure (Table 2). The parameters ‘distance to next uncolonised tree’, ‘understorey vegetation height’, ‘trunk diameter (DBH)’ and ‘position in landscape’ were removed in the stepwise model selection process. No interaction term and no quadratic term was significant. The vitality of the canopy and trunk were included in the alternative model which shows that these predictors are of great importance in predicting the occurrence probability. The parameters ‘understorey vegetation height’ and ‘DBH’ were also considered to be significant predictors of species presence so that the alternative model consisted of seven predictor variables.

**Table 2** Parameter estimates of the final logistic regression model (residual deviance =166.55 on 211 degrees of freedom, null deviance=258.97 on 215 degrees of freedom). Corresponding response surfaces are shown in Fig. 1.

	<i>Variable</i>	<i>Regression coefficient</i>	<i>SE</i>	<i>p</i>
$\beta_1$	Oak sap	2.636	0.457	<0.0001
$\beta_2$	Distance to next colonised tree	-1.081	0.357	0.0025
$\beta_3$	Sun index	0.211	0.058	0.0003
$\beta_4$	Bark depth	0.102	0.022	<0.0001
$\beta_0$	intercept	-4.491	0.921	<0.0001



**Figure 1** Bivariate response surfaces of the four predictors included in the final model. The estimated occurrence probability ( $P$ ) of *C. cerdo* is plotted against the three continuous predictors. Left and right surfaces represent the different levels of the fourth predictor. Sun index is fixed to be 6 for the first row, distance to the nearest occupied tree is 141 m in the second row. The occurrence of *C. cerdo* increases with increasing bark depth, sun index and oak sap as well as decreasing distance to the nearest occupied tree.

We conducted a hierarchical partitioning procedure to quantify the independent contribution of our predictor variables considered in the final model to the response (Fig. 2). The results show the relative importance of the presence of oak sap on the trunks (44%). Depth of the bark, which is highly correlated with trunk diameter, contributed 30% to explaining the occurrence of *C. cerdo* on the oaks, whereas the influence of the power of the sun contributed only 16% and the distance to the next colonised tree a little less than 10%. All four variables are highly significant predictors of presence of *C. cerdo*.

**Table 3** Parameter estimates of the alternative logistic regression model (residual deviance = 129.57 on 211 degrees of freedom, null deviance = 258.97 on 215 degrees of freedom).

	<i>Variable</i>	<i>Regression coefficient</i>	<i>SE</i>	<i>p</i>
$\beta_1$	Oak sap	1.790	0.499	0.0003
$\beta_2$	Canopy vitality [partly dead]	3.131	0.488	<0.0001
$\beta_3$	Canopy vitality [mostly dead]	3.873	0.776	<0.0001
$\beta_4$	Diameter	2.231	0.688	0.0012
$\beta_0$	Intercept	-5.397	0.910	<0.0001

### 3.2 Model validation

The final model explains nearly 50% of the overall variance of the response variable in our training dataset ( $R^2_{N=}$  0.498). The model also shows a high discriminative power with an AUC-value of 0.87 ( $CI_{95\%}$ : 0.82–0.92). The alternative model with seven predictors yields a considerably better general fit ( $R^2_{N=}$ 0.753) and a higher AUC of 0.96 ( $CI_{95\%}$ : 0.93–0.99). There are several classification thresholds, depending on the research goal (Table 4). To achieve the best balanced predictive performance, we used  $P_{fair}$  as the appropriate classification threshold for the final model (cf. Jiménez-Valverde and Lobo, 2006). Evaluation of kappa after Monserud and Leemans (1992) indicates fair predictive power for the final model and very good predictive power for the alternative model with a higher number of predictors.

**Table 4** Different classification thresholds and their effects on prediction success according to Schröder and Richter (1999), calculated with ROC\_AUC (Schröder 2006).

<i>Criteria</i>	<i>Final model</i>			<i>Alternative model</i>		
	$P_{fair}$	$P_{kappa}$	$P=0.5$	$P_{fair}$	$P_{kappa}$	$P=0.5$
Threshold probability $P_{crit}$	0.2775	0.515	0.500	0.400	0.460	0.500
Sensitivity	0.787	0.639	0.639	0.855	0.839	0.807
Specificity	0.779	0.929	0.909	0.863	0.902	0.902
Correct classification rate	0.781	0.847	0.833	0.861	0.884	0.874
Kappa	0.513	0.601	0.571	0.679	0.723	0.698



### 3.3 Is the habitat model transferable in space?

We validated our final model testing its transferability to an external dataset from Saxony-Anhalt. We analysed 144 oaks from different stands, of which 55 were found to be colonised and were entered into the dataset (38%). The regression equation from the training dataset was applied to predict the spatial distribution for this external test dataset. The model resulted in an AUC-value of 0.87 (CI<sub>95%</sub>: 0.83–0.93) within the test dataset. Surprisingly, there is a slightly better performance within the test data as regards the prediction of both presences and absences (Table 5). We also tested alternative model building with the dataset from Saxony-Anhalt and further validation on the data from Lower Saxony. The data from Saxony-Anhalt provided a better model, but also a poorer predictive performance in the spatial validation procedure using the Lower Saxony data. The importance of the individual parameters changed only slightly (results not shown).

**Table 5** Performance of the final model and results for the spatial validation on the test dataset. AUC (Area Under Curve) is provided as a threshold independent criterion. Threshold dependent criteria are given with respect to  $P_{\text{fair}}$  which is the classification threshold where the performance for presences (sensitivity) and absences (specificity) is nearly balanced (see also Table 4).

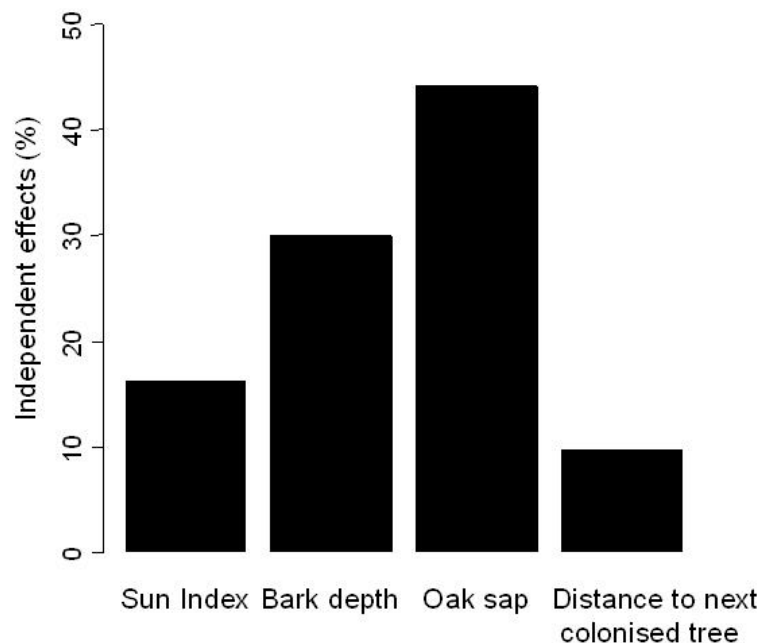
Parameter	Training data (n=216)	Test data (n=144)
AUC with 95% CI	0.87 [0.82 ... 0.92]	0.87 [0.83 ... 0.93]
Sensitivity	0.79	0.80
Specificity	0.78	0.82
Correct classification rate	0.78	0.81
Kappa	0.51	0.61

## 4 Discussion

### 4.1 Parameters describing aspects of the realised niche

Our model exhibits relevant habitat factors which are essential for habitat selection in the longhorn beetle *Cerambyx cerdo*. We are able to predict occupancy patterns in this beetle species with only a few analysed variables. Species distribution models based on field data predict the realised niche in the study area (Guisan and Zimmermann, 2000). Our results show that the bark depth of the trees is one of the significant predictors for species presence. Bark depth and trunk diameter are highly correlated. We measured colonised oaks with trunk diameters from 0.64m to 2.32 m. Increasing age and diameter of the oak trees improves the occurrence probability for

our study species. Ranius and Jansson (2000) have shown that trunk diameter is an important determinant of saproxylic species richness in common as well as rare red-listed beetles associated with oaks. Tree diameter also restricts occupancy of other highly endangered beetles (e.g. *Tenebrio opacus*, Ranius, 2002). The latter species also occurs in the research area in Lower Saxony. The bark depth also seems to be very important for successful egg development in our study species with female beetles preferentially using protected deep slits in the bark for oviposition (Döhning, 1955).



**Figure 2** Contribution of the individual predictors to the final model response (independent effects calculated by hierarchical partitioning with respect to the log likelihood as goodness-of-fit criterion).

Our alternative model considers oak vitality as a powerful predictor indicating high occurrence probabilities on trees with a large number of dead branches or damaged sections of trunk bark. The vitality of trunk and canopy appeared to be another important parameter for predicting the presence of this saproxylic beetle species. A correlative analysis such as logistic regression leads to such simple mechanistic results, but is this not a misinterpretation of causes and effects?

Müller (2001) reported oaks with physiological failings and trees with damage as a typical habitat for *C. cerdo* and Zuppke (1993) described dead branches as useful signs of presence. Our study species belongs to a small number of longhorn beetle species which are able to attack living trees (Bense, 1995). In fact, we know that the larvae of *C. cerdo* need fresh wood to feed and have become extinct on dead trees (Neumann, 1985). The larval damage to living wood strongly affects the water and nutrient supply network inside the tree, which in turn leads to the death of some branches in the canopy. This means that this beetle is effecting changes in its own essential habitat which amount to a destruction of habitat conditions for the following generations. Therefore, a low vitality of oak canopy and trunk reflects an unsuitable habitat for the larvae of *C. cerdo* and is the result of larval feeds. For this reason these parameters were not included in our final predictive habitat model.

Oak sap is sometimes suggested as an important food resource for the adults (Neumann, 1985). There are some observations showing that *C. cerdo* is attracted by oak sap on trees (Weckwerth, 1954; Döhring, 1955). Sap spots are common on most trees of the genus *Quercus*. Some species from the beetle family Nitidulidae are known for their specialisation in feeding on sap spots of different tree species (e.g. Juzwik et al., 2004; Zeran et al., 2006). These sap spots are often the door for disease infections transmitted by sap visiting insects (Ambourn et al., 2005). Our model predicts a higher likelihood of occurrence if there are oak sap spots on the tree. As Fig. 2 reveals, this is the most important predictor. Therefore, related infections may be important for the ability of *C. cerdo* to attack these weakened trees. In the case of many other saproxylic beetles (Grove, 2002; Ranius, 2006), the distance to the next colonised oak tree is a significant predictor of occurrence probability. According to Schiegg (2000) habitat fragmentation in saproxylic beetles occurs on a more local scale (<150 m). Considering that *C. cerdo* uses a transient resource there is only a poor dispersal power in this species. In search of a better prediction of occupancy we combined habitat quality, patch size and isolation to develop a model which satisfies a primary connection between the habitat and metapopulation approach in the sense of Armstrong (2005). Despite the fact that the use of all spatial scales in species distribution modelling sometimes leads to better classification results and better general fit (Johnson et al., 2002), the only significant landscape predictor is the distance to the next colonised oak. The position of the trees in the landscape does not affect occurrence probabilities. But the influence of

landscape structure is visible in the sun conditions/exposition on the trunks. It is expected that a more open landscape offers more sun-influenced trunks than a closed woodland. Surprisingly, the influence of the sun exposition of the bark is of subordinate importance for the likelihood of occupancy. This parameter gives significant changes in the outcome, but with relatively low contributions compared to the other variables. Sun-exposed trees, especially those which are south exposed seem to be favourites for colonisation. Zuppke (1993) observed oaks at the northern boundaries of woodlands where *C. cerdo* was present, and postulated that the degree to which the trees are exposed to open spaces has an additional effect on colonisation. Species richness and number of red-listed saproxylic beetles are found to be significantly higher in sun-exposed trees (Lindhe and Lindelöw, 2004). Therefore, sun-exposed trees play a major role in the conservation of many saproxylic beetles. However, the larval development of *C. cerdo*, which takes place in the interior of the trunk, is favoured by increasing insolation.

#### 4.2 Model evaluation and validation

ROC-curves are a useful evaluation tool for predictive species distribution models (see Fielding and Bell, 1997; Pearce and Ferrier, 2000; Reineking and Schröder, 2006). Because it is independent of prevalence, this technique gives an appropriate measure of accuracy (Fielding, 2002). The AUC-value of the final model indicates excellent discriminative power according to Hosmer and Lemeshow (2000). Kappa, a satisfying indicator of model predictive performance (Manel et al., 2001), ranged from 0.5 to 0.6, which indicates good predictive power (after Monserud and Leemans, 1992). One goal of our research was to analyse the general fit of the model when applied to another geographic region (see Schröder and Richter, 1999; Randin et al., 2006). The spatial validation shows similar predictive and discriminatory power to that in the model building region. This means that the model can further be applied to other geographic regions of Central Europe. There is no effect of altered habitat requirements between our tested regions for the species we investigated.

#### 4.3. Application to habitat management and implications for conservation

To facilitate survival by establishing high habitat quality for *C. cerdo*, management strategies should focus on opening up wood stands and trees. Semi-open wood

stands are thought to be suitable landscape structures. This kind of landscape also harbours a great variety of different microhabitats in dead wood, which has a strong impact on overall saproxylic species richness (Lindbladh et al., 2003; Gibb et al., 2006). *C. cerdo* depends on semi-open wood stands, which also meet the habitat requirements of *Osmoderma eremita* and some other highly endangered beetles (Ranius and Nilsson, 1997). These threatened beetle species have similar habitat requirements on the landscape level, in particular with respect to tree conditions, a fact which should be taken into account in management of nature conservation areas. Recent studies have shown that both saproxylic and species rich epigaeic insect communities (e.g. Falke et al., 2000) and the plant communities associated with natural disturbance (Poschlod et al., 2002; Mountford and Peterken, 2003) will benefit considerably from an interesting new approach involving large herbivores in wood pasture landscapes. Grazing with large herbivores, such as horses or cattle, promises the best impact to generate suitable landscape and tree-level conditions on oaks for occurrence of *C. cerdo*. Because of their ability to feed on the lower canopy branches and leaves large herbivores are important for opening the trunks to the sunlight. Surprisingly, grazing seems to be important for oak recruitment. Vera (2000) found no new young generations of oak trees in the closed forest reserves he studied. Despite the discussion about the natural landscape structure in Central Europe (closed forest vs. park landscape; see Vera, 2000) there is a distinct man-made component in the potential suitable habitats for our study species. Elements of cultural landscapes, for example tree avenues or parks, can also harbor viable populations of *C. cerdo*. A large number of today's remnants colonised by *C. cerdo* are either still or were formerly used as wood-pasture (as for instance the nature reserve 'Ochsenbusch' in Saxony-Anhalt). One problem affecting population survival of our study species in our recent landscapes is the shortage of trees with sufficient trunk diameter for colonisation and establishment of a stable population over a number of years. A large number of the recently colonised oaks in the Elbe region were planted in the past to protect the dikes against iceshore drift in winter. If this measure were to be taken up again today in the area between the dike and the river, this would help provide a large number of oaks for the future. Ranius and Jansson (2000) made valuable suggestions for the conservation of rare saproxylic beetles associated with hollow oaks. They proposed the resumption of former management

activities in areas with old oaks and a restoration of regrown sites. One of these former uses should be wood pasture which has been recommended as a successful tool in nature conservation for a number of different threatened taxa (Redecker et al., 2002). In the re-introduction of wood pasture, the focus should be on a large spatial scale and on low grazing intensity to allow for recruitment of oak seedlings (Vera, 2000) and moderate disturbance. Jonsell et al. (2004) point out the value of man-made deadwood substrate in modern forestry. Their results show that naturally created stumps can provide a greater overall species richness in the case of saproxylic beetles. Therefore, we should aim to conserve saproxylic species richness using natural processes.

## 5 Conclusion

We have shown that a habitat suitability analysis is useful for scientifically based habitat management of saproxylic species. Our research provides basic information for an evaluation of the remaining areas as well as for reserve selection in the endangered longhorn beetle *Cerambyx cerdo* in Central Europe. A derived evaluation index of trees or areas can easily be developed from our results. This would be very helpful for the next reports to the European Commission. Important results obtained from our research are the knowledge and quantification of a number of aspects of the realised niche, and of the habitat conditions necessary on tree and landscape level to maintain existing populations of *C. cerdo*. This species prefers distinct habitat conditions and this allows us to make very good predictions of its spatial distribution based on a relatively small dataset. Regarding the key function of *C. cerdo* for occurrence of other highly endangered saproxylic beetles, we are able to recommend an integrative approach for habitat management which will also be of great benefit to other taxa. The vitality of the oak trees included in the alternative model may be used in future to detect unknown presences of *C. cerdo* in the field. As a parasite of oaks, *C. cerdo* depends on a fairly large number of suitable trees in its proximity. The provision of such conditions over decades is the essential key in the conservation of this protected and highly endangered longhorn beetle species.

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# II

An endangered longhorn beetle associated with old oaks  
and its possible role as an Ecosystem Engineer

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## Abstract

For more than 10 years, ecologists have been discussing the concept of ecosystem engineering (i.e., nontrophic interactions of an organism that alters the physical state of its environment and affects other species). In conservation biology, the functional role of species is of interest because persistence of some species may be necessary for maintaining an entire assemblage with many threatened species. The great capricorn (*Cerambyx cerdo*), an endangered beetle listed in the European Union's Habitats Directive, has suffered a dramatic decline in the number of populations and in population sizes in Central Europe over the last century. The damage caused by *C. cerdo* larvae on sound oak trees has considerable effects on the physiological characteristics of these trees. We investigated the impacts of these effects on the species richness and heterogeneity of the saproxylic beetle assemblage on oaks. We compared the catches made with flight interception traps on 10 oaks colonized and 10 oaks uncolonized by *C. cerdo* in a study area in Lower Saxony (Germany). Our results revealed a significantly more species-rich assemblage on the trees colonized by *C. cerdo*. Colonized trees also harbored more red-listed beetle species. Our results suggest that an endangered beetle species can alter its own habitat to create favorable habitat conditions for other threatened beetle species. Efforts to preserve *C. cerdo* therefore have a positive effect on an entire assemblage of insects, including other highly endangered species. On the basis of the impact *C. cerdo* seems to have on the saproxylic beetle assemblage, reintroductions might be considered in regions where the species has become extinct.

## Introduction

Ecosystem engineers “control the availability of resources to other species by causing physical state changes in biotic or abiotic materials” (Jones et al. 1994). Knowledge about the engineering characteristics of species in highly threatened communities is valuable because it is particularly important that populations of ecosystem engineers be preserved. Nevertheless, the abundance of ecological engineers may be reduced to a level at which the species no longer serves an engineering function. Although a considerable amount of research has been done on ecosystem engineering (Crooks 2002; Wright & Jones 2004; Badano & Cavieres 2006; Byers et al. 2006; Jouquet et al. 2006; Wright & Jones 2006; Hastings et al. 2007), studies are still lacking for many species-rich communities, for instance, the

assemblage associated with dead wood. The European network of conservation areas, Natura 2000, focuses on the protection of species and their habitats and complex ecosystems, with the goal of conserving biodiversity, including genetic diversity and ecosystem functions. The endangered species covered by Natura 2000 are either priority species (i.e., species found exclusively in Europe that are threatened with extinction) or species that are representative of certain ecosystems. These endangered species are listed in Annex I and II of the European Habitats and Birds Directives. The decision to include these species and exclude others has been discussed and criticized (e.g., Bouchet et al. 1999; Grill et al. 2002). The Natura 2000 network also aims to include sites that maintain habitats for endangered species and harbor a high level of biodiversity (e.g., Dimitrakopoulos et al. 2004; Moilanen 2005; Deguise & Kerr 2006). Species-rich fauna and flora are associated with old trees. Of the fauna associated with old trees, woodpeckers, for example, are important to many other species, such as birds and invertebrates, because they create cavities (e.g., Jönsson et al. 1993). Furthermore, it is assumed that some saproxylic (i.e., wood-dwelling) beetle species in old trees create microhabitats favorable for other saproxylic species by enhancing the richness of nutrients, such as nitrogen (Jönsson et al. 2004), or creating galleries (i.e., holes and cavities by larval feeding) (Palm 1959); nevertheless, no systematic studies have yet tested this assumption. Saproxylic insects play a major role in the decomposition of wood and thus in nutrient cycling. Nutrient cycling means decomposition of organic material and the assimilation of nutrients by plants in general. An example is that hollows with *Osmoderma eremita* (Scarabaeidae) are richer in some nutrients (N and P) because of larval frass (Jönsson et al. 2004). Many of these insects are rare and classified as threatened in Europe because ancient and dead trees are scarce in landscapes strongly changed by humans (Speight 1989). Saproxylic beetles represent a species-rich group that has adapted to different microhabitats of wood (e.g., Palm 1959). One of these insects is the longhorn beetle *Cerambyx cerdo* (Coleoptera, Cerambycidae), which mainly occurs on living oak trees. *C. cerdo* is classified as vulnerable on the World Conservation Union Red List (World Conservation Monitoring Centre 1996) and is listed as a non priority species in the Annexes II and IV of the European Habitats and Species Directive (Council of the European Communities 1992). When a tree is attacked by *C. cerdo*, the tree may survive over long periods, but the amount of dead wood on the tree increases. Furthermore, the larvae create extensive

galleries (Palm 1959; Fig. 1), which may act as entrances and habitats for other species (e.g., *O. eremite* [Scarabaeidae] or *Tenebrio opacus* [Tenebrionidae]). For this reason, the species may be an ecosystem engineer that affects the saproxylic assemblage associated with dead wood on trees that still are alive. We investigated the physical impact of *C. cerdo* on old oaks and on the number of saproxylic beetle species living in those trees. This was done by correlating species richness of the saproxylic beetle fauna, different tree characteristics, and presence and absence of *C. cerdo* with each other. Strong positive correlations between occurrence of *C. cerdo* and richness of the entire saproxylic beetle fauna suggest that the presence of this species could be used as an indicator of species richness of saproxylic beetles. If the correlation seems to be due to the fact that *C. cerdo* may alter the habitat for other species, it suggests that the species is an ecosystem engineer. In such a case, persistence of existing populations and, if possible, reintroductions of the species are important goals in nature conservation.



**Figure 1** Galleries on oaks colonized and fed on by *C. cerdo* larvae. The left panel shows emergence holes and places where underbark feeding occurred (photo by R. Axelsson from Ehnström & Axelsson 2002). The right panel depicts larval galleries inside the trunk and shows that the larvae also explore the inner parts of the trunk.



## Methods

### *The study species*

The larval development of *C. cerdo* takes place in fresh wood, mainly oaks (*Quercus* spp.) and lasts 4 to 5 years (Neumann 1985). In Central Europe the larvae usually develop in *Q. robur* or *Q. petraea*, whereas in its southern distribution there are records of larvae from *Q. pubescens*, *Q. ilex*, *Q. suber*, *Q. calliprinos*, and *Castanea sativa* (Luce 1997). Suitable trees have a sun-exposed trunk at least 60 cm in diameter (Buse et al. 2007). Adult beetles emerge in June and July. They are mainly nocturnal and have a lifetime of a few days up to 2 months (Neumann 1985). The dispersal biology of the species is poorly known, but considering the short life span of the adults and that it flies mainly after dusk when the temperature exceeds 18° C (Neumann 1985), their dispersal ability is probably limited. *C. cerdo* is relatively widespread in Europe, northern Africa, and the Middle East, but has become extinct in, for instance, the United Kingdom (Alexander 2002) and the Swedish mainland (Ehnström & Axelsson 2002). Over the last century, the species has suffered a dramatic decline in the number of populations and in population sizes in Central Europe (Klausnitzer et al. 2003). This is mainly due to a decline in the number of old oak trees situated in open or semiopen landscapes (Luce 1997). Changes in landscape structure as a result of altered agricultural and forest management practices have led to a decline in potential habitats for this longhorn beetle species. The species is protected under the EU Habitats Directive. Beetle species mentioned in the EU Habitats Directive are in general relatively large-sized insects with a distinct flagship role (cf. Simberloff 1998). Besides these species, there are, however, many tiny species that may be in greater danger of extinction, but because they are unattractive to the public and are difficult to identify they are not listed in the Habitats Directive.

### *Study area*

Our study area was in the Gartower Elbmarsch (53° 1'N, 11° 27'E), where the last population of the longhorn beetle *C. cerdo* in Lower Saxony (Germany) occurs. The Gartower Elbmarsch is characterized by large pastures interspersed with groups of trees and small woodlands. Most trees on which *C. cerdo* occur are in a narrow strip of pasture between a dike and the river Elbe and along a 3-km long avenue with a

mixture of oak trees of different ages on both sides. The area is part of the Man-and-Biosphere Reserve River Landscape Elbe.

### ***Insect data and environmental variables***

We used interception traps of the same type as Hyvärinen et al. (2006) (but with a protective cover against rainfall) to survey the flight-active beetle fauna of the oak trees. The perpendicular, crossed windows in the traps each measured 30 × 50 cm. The traps were placed in the lower canopy, 4–5 m above ground, from 10 May to 28

August 2006. We used preserving agent in the traps (Renner 1980) and emptied the traps at 3-week intervals. We identified all captured beetles to species level. In our analyses, we included only species that are saproxylic and develop in living or dead oak wood according to Palm (1959) and Schmidl and Bussler (2004). The same literature was used to classify the species into 6 feeding guilds (mycetophagous, necrophagous, polyphagous, succiphagous, xylophagous, zoophagous) to analyze differences in the richness of these feeding guilds in the beetle assemblage. The red-list classification was taken from the national Red List of Germany (Geiser 1998). Individual trees used for trapping were selected randomly from a pool of 216 oaks investigated previously (Buse et al. 2007). In total we surveyed 10 colonized and 10 uncolonized trees. The only limitations on selection were that all uncolonized trees investigated be at least 30 m from the nearest colonized tree and have a diameter >50 cm. Uncolonized trees were at least 15 m apart. To compare the colonized and uncolonized trees, we measured a set of tree characteristics that might affect the saproxylic fauna (Table 1). To give a more general view of the difference between trees with and without *C. cerdo*, we also used data from 216 sampled oaks in the broader study region (Buse et al. 2007).

### ***Statistical analyses***

We corrected the number of saproxylic species for each tree with the rarefaction procedure for continuous sampling (after Hurlbert 1971), which uses the sample with the smallest number of individuals in each group as reference. Simpson's diversity index ( $D$ ) was used to compare the heterogeneity of the saproxylic assemblage between colonized and uncolonized trees. By taking relative abundances into

account, this diversity index indicates species richness and the evenness, or equitability, with which individuals are distributed among the different species.

**Table 1** Variables measured from oaks colonized and uncolonized by the longhorn beetle *C. cerdo* in northern Germany

<i>Measured variables</i>	<i>Colonized trees</i> (number of cases or mean)	<i>Uncolonized trees</i> (number of cases or mean)	<i>Test for differences</i> ( <i>p</i> ) <sup>a</sup>
Canopy vitality	7 mostly or partly dead; 3 living	0 mostly or partly dead; 10 living	0.003 ** (Fisher's exact test)
Colonization intensity (on the trunk up to a height of 2.5 m)	2 with 1-10 holes; 6 with 11-30 holes; 2 with >30 holes	-	-
Oak sap	4 with no sap locations; 6 with sap location(s)	9 with no sap locations; 1 with sap location(s)	0.057 (Fisher's exact test)
Position in landscape	1 solitary; 1 at woodland edge; 4 at a patchy site; 4 at an avenue	0 solitary; 3 at woodland edge; 1 at a patchy site; 6 in an avenue	-
Sun exposure	[0=heavily shaded, no direct sun] to [12=sun from all directions] on the trunk mean=8.2	[0=heavily shaded, no direct sun] to [12=sun from all directions] on the trunk mean=3.7	0.001 *** (Wilcoxon rank-sum test)
Trunk diameter (DBH <sup>b</sup> )	Measured at breast height in [m] mean=1.27 m	Measured at breast height in [m] mean=0.88 m	0.006 ** (Wilcoxon rank-sum test)
Trunk hollows with entrance > 5 cm	6 with trunk hollows; 4 with no trunk holes	1 with trunk hollows; 9 with no trunk holes	0.057 (Fisher's exact test)
Trunk vitality	7 with dead barkless parts; 3 with vital bark	2 with dead barkless parts; 8 with vital bark	0.069 (Fisher's exact test)

<sup>a</sup> \*\**p* < 0.01; \*\*\**p* < 0.001.

<sup>b</sup> Diameter at breast height

As recommended by Krebs (1999), we used the reciprocal of *D* to test differences in the means with Student's *t* test. Raw species numbers were used to compare the number of red-listed beetle species and to analyze differences in richness between the two groups of trees in the feeding guilds. We applied the Wilcoxon rank-sum test to investigate differences in the median. We used Spearman's rank correlation

coefficient to explore relationships between the rarefied species richness and the set of possibly explanatory variables measured from the trees. Strong correlations between the independent variables made it impossible to conduct a multiple regression analysis (cf. Crawley 2005). We ran a hierarchical partitioning procedure to reveal the total independent contribution of each parameter to overall species richness (Mac Nally & Walsh 2004). This method can be used to overcome the problem of multicollinearity in a data set (Mac Nally 2000). We used  $R^2$  as the goodness of-fit criterion. Fisher's exact test was used to compare the number of species occurrences between colonized and uncolonized trees. We used the same test to show differences in measured tree characteristics between our 2 groups of oaks. Rarefaction was performed with a calculator devised by J. Brzustowski (<http://www2.biology.ualberta.ca/jbrzusto/rarefact.php>), which is based on the program RAREFACT.FOR written by C. J. Krebs. We carried out all other statistical analyses with R 2.2.0 (R Core Development Team 2005).

**Table 2** Spearman's rank correlation coefficient for the variables measured on 20 studied oak (*Quercus robur*) trees.<sup>a</sup>

	Species richness <sup>b</sup>	Canopy vitality	Colonization intensity	Oak sap	Sun exposure	Trunk diameter	Trunk hollows	Trunk vitality
Species richness	x	-0.577** <sup>c</sup>	0.745*** <sup>d</sup>	0.656*** <sup>d</sup>	0.505* <sup>c</sup>	0.372	0.355	-0.559* <sup>c</sup>
Canopy vitality		x	-0.757*** <sup>d</sup>	-0.576** <sup>c</sup>	-0.535* <sup>c</sup>	-0.064	-0.293	0.333
Colonization intensity			x	0.494*	0.507* <sup>c</sup>	0.503* <sup>c</sup>	0.573** <sup>c</sup>	-0.625** <sup>d</sup>
Oak sap				x	0.305	0.136	0.341	-0.389
Sun exposure					x	-0.099	0.055	-0.229
Trunk diameter						x	0.700*** <sup>d</sup>	-0.488*
Trunk hollows							x	-0.390

<sup>a</sup> "Position in the landscape" was not considered here because it is scaled in multinomial classes. Significance levels are \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ .

<sup>b</sup> Species richness of saproxylic beetles.

<sup>c</sup> Correlations stronger than 0.5.

<sup>d</sup> Correlations stronger than 0.6.

## Results

We identified 7225 individuals from 181 saproxylic beetle species in 41 families. Sixty-nine of these beetle species are listed in the national Red List of Germany. *Xyleborus saxeseni*, a common bark beetle, constituted more than half of the entire sample, whereas 49 species were recorded as single individuals. Among all recorded species, 4 beetle species were strongly ( $p < 0.01$ , Fisher's exact tests) associated with oaks colonized by *C. cerdo*: *Euglenes oculatus* (Aderidae), *Dorcatoma flavicornis* (Anobiidae), *Globicornis nigripes* (Dermestidae), and *Prokraerus tibialis* (Elateridae). Sixty-three beetle species (including 31 red-listed species) from 23 families were exclusively recorded on oaks with *C. cerdo*. Twenty-nine of the single individuals were recorded only on oaks with *C. cerdo*. At least 9 of these exclusive species are primarily hunters on barkless parts of the trunk (e.g., *Colydium filiforme* [Colydiidae], *Dermestoides sanguinicollis* [Cleridae], and *Corticeus* spp. [Tenebrionidae]). Four other predatory species exclusively recorded from colonized oaks live in tree hollows (e.g., *Brachygonus megerlei* and *Ampedus cardinalis* [both Elateridae]). In comparison, 25 beetle species (including 5 red-listed species) were exclusively recorded on trees without *C. cerdo* colonization. None of these had a statistically significant association with these oaks, and 20 of these 25 species were single individual records.

### **Differences between colonized and uncolonized trees**

On average, oak trees colonized by *C. cerdo* had a lower canopy vitality and a larger girth and were more exposed to the sun compared with uncolonized trees (Table 1).

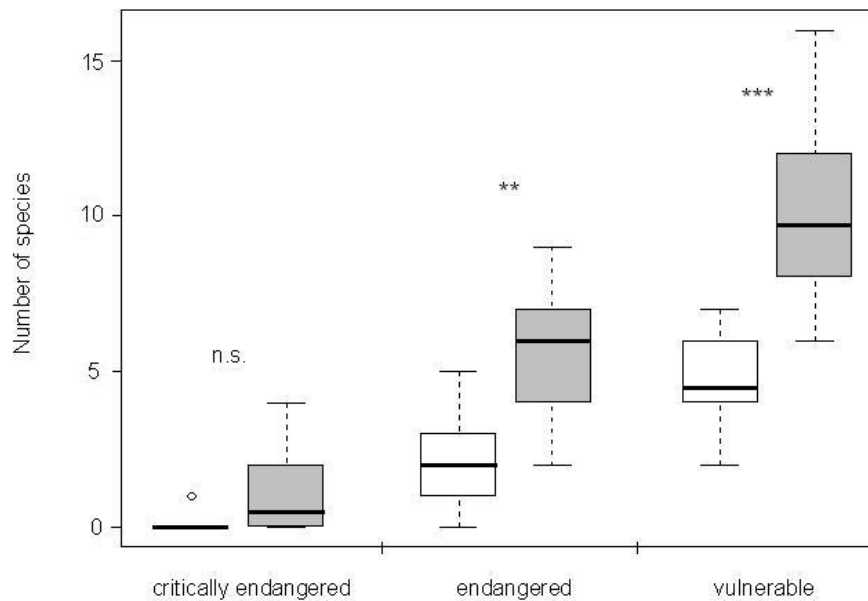
The main difference between colonized and uncolonized trees was the amount of dead wood. Nearly 20% of all colonized trees ( $n=63$ ) in the broader study area had a canopy that was largely dead, whereas this was the case for only 2% of the uncolonized trees ( $n=154$ ) (Buse et al. 2007). This difference was strongly significant ( $p < 0.001$ , Fisher's exact test). In addition, more than 60% of all colonized trees had at least a number of branches thicker than 10 cm that were mostly dead, whereas among uncolonized trees the corresponding figure was 12% ( $p < 0.001$ , Fisher's exact test). More than 30% of the colonized trees had dead, barkless parts, compared with only 5% in the case of uncolonized oaks ( $p < 0.001$ , Fisher's exact test).

### ***Species richness of the saproxylic assemblage***

The number of species differed significantly between colonized and uncolonized trees for the various sample sizes. Overall, rarefied species numbers ranged from 15 to 34 (mean=23) on uncolonized and from 27 to 37 (mean=33.1) on colonized trees ( $p < 0.002$ , Wilcoxon rank-sum test). The colonization intensity of *C. cerdo* was the parameter with the strongest correlation with overall richness of rarefied beetle species on our investigated oaks (Table 2). Occurrence of oak sap and reduced trunk and canopy vitality (i.e., large amounts of dead wood) was also strongly correlated with species richness. Nevertheless, tree diameter was only weakly related to the number of beetle species. A hierarchical partitioning of the tested parameters emphasized the relevance of the colonization intensity (independent contribution of 24%) on overall species richness. The occurrence of oak sap spots (22%) and sun exposure (16%) also seemed to be important determinants of the overall number of saproxylic beetles on the analyzed trees. The diameter of the oaks (11%), canopy vitality (11%), trunk vitality (9%), and occurrence of trunk hollows (6%) showed only a weak impact on species richness. Trees colonized by *C. cerdo* harbored more red-listed species in all IUCN categories than was the case for uncolonized trees (Fig. 2). A particularly strong difference between the two groups of trees was observed in the number of endangered and vulnerable beetle species.

### ***Heterogeneity of the saproxylic assemblage***

Communities on both colonized and uncolonized oaks showed a similar pattern in the relationship between species and their abundances. Only a few species were abundant, and most species occurred in low numbers. Species for which we found only one specimen represented a large proportion of the species in both groups of trees. The values of Simpson's index of diversity ( $1/D$ ) as a measure of the heterogeneity of the sampled assemblage for both groups were significantly different: colonized trees (mean  $1/D = 4.8$ ) harbored a more heterogeneous saproxylic assemblage than uncolonized trees (mean  $1/D = 2.4$ ; Student's  $t$  test,  $p = 0.002$ ). The heterogeneity of the communities was not correlated with the diameter of the oak trees (Spearman's rank correlation coefficient,  $r = 0.266$ ,  $p = 0.257$ ).



**Figure 2** Number of saproxylic beetle species captured on trees that were colonized and uncolonized by *C. cerdo* that are recorded in the national Red List of Germany and classified according to the World Conservation Union criteria as critically endangered, endangered, or vulnerable. Shaded bars indicate colonized trees (n=10), and unshaded bars represent uncolonized trees (n=10). The horizontal lines show the median, 25% and 75% quartiles, and the dashed lines indicate the range of the data. Differences were tested with the Wilcoxon rank-sum test: critically endangered,  $p=0.118$ ; endangered,  $p=0.003$ ; vulnerable,  $p=0.001$  (\*\* $p < 0.01$ ; \*\*\* $p < 0.001$ ; n.s. = not significant).

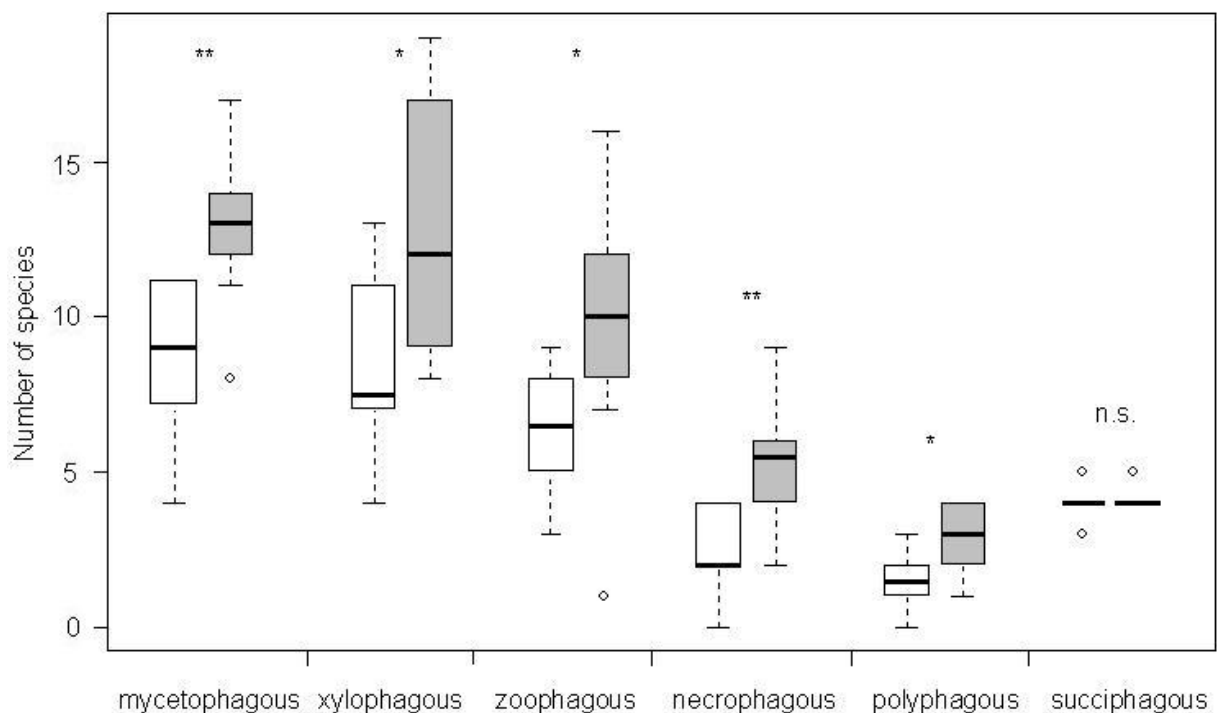
### **Impact on Functional Traits**

We identified 6 feeding guilds in the saproxylic beetle assemblage. Most species feed on wood (xylophagous), fungi, or fungi-infested wood (mycetophagous) or were predators (zoophagous). In terms of the number of species present, trees with *C. cerdo* had more beetle species in all feeding guilds, with the exception of beetles feeding on sap streams (Fig. 3). We also analyzed the number of individuals per feeding guild in the 2 groups of trees. Necrophagous (Wilcoxon rank-sum test;  $p=0.005$ ), xylophagous ( $p=0.019$ ), and zoophagous ( $p=0.034$ ) individuals were significantly more abundant on oaks colonized by *C. cerdo*.

### **Discussion**

Trees colonized by the endangered longhorn beetle *C. cerdo* harbored a more species-rich and heterogeneous beetle fauna than uncolonized oaks. Furthermore, there were large differences in physiological characteristics between colonized and uncolonized trees. This suggests that the main reason species richness was higher in colonized trees may be that *C. cerdo* considerably alters the physiological

characteristics of its host tree when the larvae feed on the wood. An alternative explanation is that *C. cerdo* may colonize trees with injuries more easily than completely sound trees, which potentially generates a difference between colonized and uncolonized trees not caused by the activity of *C. cerdo*. The extensive occurrence of dead wood with galleries caused by the *C. cerdo* larvae makes it likely that the first explanation is most probable. A third explanation is that trees with *C. cerdo* are on average more species rich, larger, and more exposed to the sun because *C. cerdo*, as well as a significant proportion of the saproxylic beetle fauna, prefers such trees (cf. Ranius & Jansson 2000). Nevertheless, species richness was more strongly correlated with the intensity of *C. cerdo* colonization than with sun exposure or trunk diameter (Table 2), which indicates that *C. cerdo* colonization is the cause of the species richness rather than other habitat-quality variables. The intensity of colonization by *C. cerdo* also represents the most important independent effect on the overall number of saproxylic beetles.



**Figure 3** Number of saproxylic beetle species per feeding guild found on oaks colonized (shaded, n=10) and uncolonized (unshaded, n=10) by *C. cerdo*. The horizontal lines show the median, 25% and 75% quartiles, and the dashed lines indicate the range of the data. Differences were tested with the Wilcoxon rank-sum test: mycetophagous, p=0.001; necrophagous, p=0.003; polyphagous, p=0.011; succiphagous (feeding on sap streams), p=0.357; xylophagous, p=0.012; zoophagous, p=0.015 ( \*\*p < 0.01; \*p < 0.05; n.s. = not significant).



Dead wood with large emergence holes and galleries is one kind of habitat created by *C. cerdo* larvae. This may explain why predatory species, such as *Colydium filiforme*, *Colydium elongatum*, and *Corticeus fasciatus*, which use barkless parts of the trunk and emergence holes from other wood-boring species for hunting, were more frequent on colonized oaks. The darkling beetles (Tenebrionidae) *Uloma culinaris* and *Corticeus bicoloroides* also inhabit larval galleries (Palm 1959), and in our study were found them only on trees with *C. cerdo* present. This suggests that *C. cerdo* may be an ecosystem engineer that is important for many other saproxylic invertebrate species associated with old oaks. It is assumed that *C. cerdo* uses the same tree for up to several decades (Ehnström & Axelsson 2002). Furthermore, the galleries of the larvae usually persist longer than the local *C. cerdo* population on the given tree. For instance, in our study area, there were more than 50 oaks in which *C. cerdo* was no longer present, but there were signs of previous activity of *C. cerdo*. Some of the trees had been dead for many years, but were still valuable for the saproxylic fauna. Thus, colonization by *C. cerdo* may affect the dead-wood-dependent assemblage over at least a few decades.

## Conclusion

As a result of the difficulties involved in surveying and identifying many species in the saproxylic assemblage, conservationists attempted to identify surrogates of species richness. The charismatic and easily identified species that are priority species in the EU Habitats Directive may act as such surrogate species, but this idea has often been criticized (e.g., Bouchet et al. 1999; Grill et al. 2002). *C. cerdo* is listed in Annexes II and IV of the Habitats Directive because of its threatened status all over Europe (Luce 1997). It has, nevertheless, been unclear whether this beetle provides conditions favorable for other saproxylic insects. Our results suggest that *C. cerdo* may be used as an indicator of species richness for the saproxylic beetle fauna on oaks. Its usefulness as an indicator species is also supported by the fact that it is very easy to identify trees with *C. cerdo*, whereas detailed surveys of saproxylic beetles are expensive (Juutinen et al. 2006). In regions where *C. cerdo* has become extinct, it might be useful to try to reintroduce the species because it may increase the persistence probability of other threatened species by increasing the available habitat. To be useful, reintroductions should be conducted only in landscapes with a

number of old trees sufficient for the persistence of *C. cerdo*. One reason the species has declined is that potential host trees have become too shaded, due to abandoned management in oak pastures. At sites affected by forest regrowth, removal of bushes and younger trees has led to an increase in the *C. cerdo* population (Ehnström & Waldén 1986). Grazing by large herbivores also seems to be an appropriate means of opening closed forests (Vera 2000). Thus, if necessary, the reintroductions should be conducted in combination with efforts to restore the habitat. A possible disadvantage of such reintroductions is that *C. cerdo* may reduce the life time of the colonized trees. For this reason we cannot exclude the risk that the availability of old, living trees might decrease some decades after *C. cerdo* has colonized a stand of oaks. This risk calls for care when reintroducing the species, especially in small stands of old oaks.

Even if a species has proven useful as an indicator species under certain circumstances, there is a risk that it will be less useful in another situation (Kalwij et al. 2005). It is preferable to focus on indicator species with hypothesized assemblage importance because it is likely that the mechanism creating higher species richness will act in a wide range of different regions and circumstances. Our results suggest that *C. cerdo* may act as an ecosystem engineer, creating habitats for many other species. For this reason, *C. cerdo* may be a possible indicator throughout its distribution range; this, however, needs to be verified by further research. In general terms, knowledge about ecosystem engineers and responsive ecosystems should be used as far as possible to achieve more ecosystem-based nature conservation.

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# III

The role of habitat fragmentation and habitat  
configuration for the composition of saproxylic beetle  
assemblages inhabiting oaks

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## **Summary**

Aspects of habitat configuration and fragmentation have been shown to affect many animal and plant taxa. Previous studies have rarely analysed both aspects in combination with one another, and studies on the proportional impact of fragmentation and habitat configuration on diverse taxa are still lacking. To obtain insight into assemblage structure and species richness under changing fragmentation and habitat parameters we studied saproxylic beetle assemblages, a species-rich group of invertebrates, on 28 oaks standing either singly or in woodlands. Overall rarefied species richness was most influenced by habitat parameters, and solitary oaks showed a higher diversity, including even endangered species, of saproxylic beetles. Nevertheless, some habitat and trophic guilds did respond to changes in landscape structure. High-ranked trophic groups, e.g. zoophagous beetles, were found to be negatively affected by habitat fragmentation. Isolation from other trees is also partly responsible for differences in microclimate and other habitat conditions in the case of saproxylic beetles. We conclude that both solitary oaks and woodlands are essential when focussing on conservation of the entire saproxylic assemblage living on oaks. The establishment of solitary oaks as a management approach for future decades and centuries is discussed with respect to the value of such trees for conservation.

## **1 Introduction**

Habitat configuration and fragmentation are among the basic determinants of species distributions and may therefore influence the extinction dynamics of single species and may have considerable impact on community richness, composition and structure (Hunter 2002; Saunders et al. 1991). Theoretical model approaches discuss fragmentation as a spatial problem with a focus on limitations for dispersal, while empirical studies have found that fragmentation is caused primarily by habitat degradation as a result of changing habitat conditions (Harrison & Bruna 1999). Only a few studies have analysed both habitat conditions and fragmentation parameters (e.g. Thomas et al. 2001). Most studies have shown that fragmentation processes have a negative impact because, for instance, there is an increased extinction risk for populations in fragmented habitats (Debinsky & Holt 2000; Saunders et al. 1991; Stephens et al. 2004). Habitat configuration, particularly the structural diversity seen



in patches, was found to be positively associated with species richness in invertebrate communities (Økland et al. 1996; Siemann et al. 1998).

In general, but especially for nature conservation and for ecological models, it is important to know the proportions of habitat and fragmentation parameters, and particularly to understand the interaction processes between these factors. Observed patterns of species sensibility to fragmentation cover a wide range and are determined by species-specific or group traits (Driscoll & Weir 2005). Arthropod assemblages tend to respond to fragmentation within relatively short time scales (Debinsky & Holt 2000; Didham et al. 1998), because many species show low dispersal abilities and have a short life-cycle. It is interesting to analyse the impact of habitat fragmentation and habitat configuration on a species-rich invertebrate group with several trophic groups and habitat guilds. Saproxyllic (=dead wood-related) beetles fulfil these criteria and are among the important ecological groups responsible for decomposition processes in woodlands with a large number of red-listed species (Speight 1989). Because of their species richness and habitat specificity they are considered an indicator group for dead wood structures and decay stages. There is still a need for studies on community structure and richness to test recent theoretical hypotheses, e.g. the trophic rank hypothesis in species–area/species–distance relationships (Holt et al. 1999). In addition to testing this hypothesis, we provide information for conservation managers who need data and results from comparative studies in the field to make decisions on how to manage and develop existing reserves. Details on patterns of biodiversity in differently structured landscapes and knowledge about the sensitivity of certain animal taxa are needed to focus conservation efforts in the field.

The aim of our paper is to study the impact of habitat fragmentation and configuration on the richness and composition of saproxyllic beetle assemblages. This was done by comparing the catches made using flight interception traps placed in the lower canopies of oak trees, either standing as single, isolated trees or grouped together, e.g. in woodlands. This enabled us to quantify differences in the assemblage caused by both habitat parameters and structural parameters such as isolation. Our results may also be helpful in assessing the impact of habitat fragmentation on saproxyllic beetles, a hyperdiverse group of insects of considerable conservation interest.

## **2 Methods**

## **2.1 Model ecosystem**

The pedunculate oak *Quercus robur* is an important species in Central Europe both where it occurs as a solitary tree and in woodlands, and has occurred throughout the region for over 9000 years (Brewer et al. 2002). Solitary single oaks represent the smallest, most fragmented habitat that can be used as habitat and for reproduction by saproxylic insects. In general, oaks harbour a large number of saproxylic beetles, as living oak trees have a greater amount of different qualities of dead wood than other tree species (Palm 1959). Interestingly, solitary trees are considered as keystone structures in many natural and man-modified ecosystems (Manning et al. 2006). They represent, for instance, a valuable foraging habitat for insectivorous bats (Lumsden & Bennett 2005). Pollard oaks and old trees in pasture woodlands represent valuable habitats for many insects because of their large diameter and diverse wood-structures (Alexander 1998).

## **2.2 Research area**

Our study area is located in the 'Gartower Elbmarsch' (53° 1' N, 11° 27' E), a landscape characterised by pastures and meadows interspersed with groups of solitary trees and adjacent woodlands. At least parts of some of the woodlands are sometimes flooded by the nearby River Elbe and are used for extensive, sustainable forestry. We also studied trees standing in the ancient "Elbholz" woodland, one of the last remaining semi-natural floodplain woodlands in Central Europe. Most of the solitary trees studied are found in cattle and sheep pastures. Our research area is part of the MAB (Man-and-Biosphere)-reserve "River landscape Elbe".

## **2.3 Insect data and environmental variables**

We used flight interception traps of the same type as (Hyvärinen et al. 2006) (but with a protective cover against rainfall) to survey the flight-active beetle fauna of the oak trees. The perpendicular, crossed windows in the traps each measured 50 x 30 cm. The traps were placed in the lower canopy, 4-5 metres above ground, from April 27 to August 31, 2007. We used a preservation agent (ethanol, glycerine, water, acidic acid) as employed by Renner (1980) and emptied the traps at two-week intervals. We identified all captured beetles to species level. In our analyses we included species that are saproxylic (Speight 1989) and develop in oak wood, as described by Palm (1959), Köhler (2000) and Schmidl & Bussler (2004). The same literature was used to

classify the species into eight feeding guilds (mycetophagous; necrophagous; xylophagous; zoophagous; xylo- and saprophagous; saprophagous; xylomycetophagous; xylo- and zoophagous). A second classification into six habitat guilds (lignicolous; nidicolous; corticolous; xylo-detriticolous; polyporicolous; succicolous) was made according to the beetles' substrate preferences. The red-list classification was taken from the national Red List of Germany (Geiser 1998).

We studied tree characteristics and the saproxylic beetle fauna of two groups of trees: free-standing, solitary and grouped, woodland oaks. In total we surveyed 28 trees, 14 in each group. Trees used for trapping were selected in the field with respect to their landscape position and diameter. As previous literature has shown the positive relationship between saproxylic species richness and age of oak trees, we tried to select oaks similar in diameter for both groups. Nevertheless, there is a shortage of old oaks larger than one meter in diameter in recent woodlands. On the other hand, the only solitary oaks in the study region are very old oaks. To compare solitary and woodland trees, we measured a set of tree characteristics that might affect the saproxylic beetle fauna (Table 1). We used a digital lux meter to analyse the direct insolation on the trunk (Engelbrecht & Herz 2001). This was done by taking one measure on each of the oak trunks facing the sun and a second measure on a place in the sun used as a reference. Further analyses were calculated with these relative values of light intensity. To study the impact of isolation on the saproxylic assemblages we measured the distance to the next oak tree and the distance to the next woodland with the help of aerial photographs. Woodlands are defined as a group of at least 10 trees with a maximum distance of 10 m between trees.

#### **2.4 Statistical analysis**

We corrected the number of species for each tree with the rarefaction procedure for continuous sampling to compare the species richness of different sized samples (Hurlbert 1971; Krebs 1999). All samples were corrected for a collection of 100 individuals per tree. Raw species numbers were used to compare the number of red-listed beetle species and to analyse differences in the richness of feeding guilds and species with habitat preferences. We applied Shapiro-Wilk-tests to test for a normal distribution in the data. For normally distributed data we calculated t-tests to test for differences between the group of solitary and woodland oaks (Crawley 2005). To analyse the community structure of solitary oaks in comparison to woodland oaks,

the species data (28 trees x 172 species) were subjected to detrended correspondence analysis (DCA), using the MVSP program (Kovach 2007). Data were square-root transformed and rare species were down weighted (Jongman et al. 1995). In a second step we calculated Spearman rank-correlation coefficients between each axis and the measured environmental characteristics of the oaks.

We ran a hierarchical partitioning procedure to determine the total independent contribution of each parameter to assemblage attributes, such as species richness or abundance, and to identify important parameters influencing the proportion of single habitat and feeder guilds in the saproxylic beetle assemblage (MacNally & Walsh 2004). We used  $R^2$  as the goodness-of-fit criterion. Fisher's exact test was used to compare the number of species occurrences between solitary and woodland trees. We used the same test together with the t-test (or Wilcoxon rank-sum test) to show differences in measured tree characteristics between our 2 groups of oaks.

Rarefaction was performed with a calculator devised by J. Brzustowski (<http://www2.biology.ualberta.ca/jbrzusto/rarefact.php>), which is based on the program RAREFACT.FOR written by C. J. Krebs. We carried out all other statistical analyses with R 2.2.0 (R-Core-Development-Team 2005).

### **3 Results**

#### ***3.1 Differences in tree characteristics between solitary and woodland trees***

Solitary oaks differ from those standing in closed woodland in terms of shape and other characteristics (Table 1). Single free-standing trees are usually smaller with respect to height, and branches begin at a lower trunk height level than for woodland trees. In our case, solitary oaks also had a larger girth. Typical dead wood structures, such as the number of larger dead branches, barkless wood and fungi-infested parts are less frequent on woodland oaks. Solitary oaks have a more sun-exposed trunk, but occurrence of tree hollows does not differ significantly between solitary and woodland oaks.

#### ***3.2 Species richness on solitary and woodland oaks***

We identified 8520 individuals from 172 species on the 28 oaks investigated (40 species were singletons). Fifty-eight of these beetle species are listed in the national Red List of Germany. There were 4097 individuals from 144 species found on the

solitary trees (43 species were singletons). On the woodland trees we trapped 4423 specimens from 136 species (47 species were singletons). The most abundant species was the bark beetle *Xyleborus saxeseni*, which constituted 30 % of the entire sample.

Among all recorded species, three beetle species were associated ( $p < 0.05$ , Fisher's exact tests) with solitary oaks: *Hedobia imperialis* (Anobiidae), *Euglenes oculatus* (Aderidae) and *Dasytes plumbeus* (Melyridae). Furthermore, five beetle species showed a slight preference ( $p < 0.1$ , Fisher's exact tests) for solitary oaks: *Oligomerus brunneus* (Anobiidae), *Ptilinus pectinicornis* (Anobiidae), *Cortodera humeralis* (Cerambycidae), *Tillus elongatus* (Cleridae) and *Anisoxya fuscula* (Melandryidae). None of the recorded species was associated with woodland oaks (Fisher's exact tests). Several species were caught on each of the investigated oaks: e.g. *Litargus connexus* (Mycetophagidae), *Hylecoetes dermestoides* (Lymexylonidae), *Soronia grisea* (Nitidulidae), *Xyleborus saxeseni* (Scolytidae), *Atheta euryptera* (Staphylinidae).

We identified between 29 and 60 saproxylic beetle species per oak tree. On average more saproxylic beetle species were recorded on solitary oaks (mean=43.4) than woodland oaks (mean=38.3). The rarefied number of species ranged from 14.6 to 32.5 and differed significantly between solitary (mean=26.1) and woodland (mean=22.9) trees ( $p < 0.019$ , Wilcoxon rank-sum test). Oaks colonised by *Cerambyx cerdo* (old or new signs of presence) showed on average higher values (mean=27.5,  $n=5$ ) for rarefied species richness than all other solitary oaks (mean=25.2,  $n=9$ ).

### **3.3 Assemblage structure and composition**

The first three axes of the detrended correspondence analysis of saproxylic beetle assemblage composition explained 27 % of the total variance (Fig. 1). The first axis (Eigenvalue 0.12, 13 % of explained variance) was significantly positively correlated to tree diameter ( $r_s=0.712$ ), occurrence of tree hollows ( $r_s=0.617$ ), distance to the next tree ( $r_s=0.554$ ), colonisation by *Cerambyx cerdo* ( $r_s=0.537$ ), distance to next tree group ( $r_s=0.483$ ) and occurrence of barkless wood ( $r_s=0.421$ ), and is negatively correlated to tree height ( $r_s=0.455$ ). The second axis (Eigenvalue 0.08, 9 % of explained variance) was significantly positively correlated to distance to next tree group ( $r_s=0.551$ ) and negatively correlated to the height of the lowest branch ( $r_s=-$

0.504). Both axes together separate the group of solitary oaks from woodland oaks based on saproxylic beetle assemblage composition.

In order to obtain the total independent contribution of each parameter to the number of species per tree, number of specimens and to rarefied species richness per tree, we applied a hierarchical partitioning procedure. Results obtained for the number of species identified on the oaks are different from those obtained for rarefied species richness. The hierarchical partitioning procedure revealed a set of 3 parameters important for rarefied species richness. The most important parameters for rarefied species richness are the amount of dead wood on the tree (10 % explained independent contribution), the number of hollows (13 %) present on the trunk and insolation of the trunk (11 %) (Table 2). For the number of species caught per tree, we found that the diameter of the oaks plays the dominant role (23 %), followed by the number of hollows per tree (14 %). The number of specimens per tree is affected by a couple of parameters, the most important being the amount of dead wood on the oaks (22 %), occurrence of barkless wood (18 %) and tree diameter (13 %).

The overall contribution of fragmentation parameters (landscape position, distance to next tree, distance to next tree group) on the saproxylic beetle assemblage is less important than the other habitat variables combined (Table 2).

### ***3.4 Species richness in habitat guilds, trophic groups and number of red-listed species***

We classified the beetle species into six different habitat preference types (see Material and Methods). Lignicolous and corticolous species are the dominant groups in terms of species richness (Fig. 2). These two habitat guilds showed different proportions of species richness on solitary and woodland oaks. We found that lignicolous species have a larger proportion of species richness on solitary oaks, whereas corticolous species shared a larger proportion on woodland oaks. Other habitat guilds showed no difference in the shared proportions of species richness between solitary and woodland oaks. The analysis of factors influencing lignicolous species showed that they are most affected by the height of the lowest branch on each tree (21 % explained independent contribution, hierarchical partitioning) and insolation (15 %) of the trunk. Corticolous species are most affected by the distance to the next tree (25 %) and the tree diameter (16 %).

We classified the beetle species into eight different trophic guilds. Zoophagous, xylophagous and mycetophagous beetle species are the dominant groups in terms of species richness (Fig. 3). Xylophagous and zoophagous guilds showed different proportions of species richness in solitary and woodland oaks. Zoophagous species have larger proportions in terms of species richness on woodland oaks, whereas xylophagous species have larger proportions on solitary oaks. Xylophagous species are most affected by the position of the oaks (24 %; whether single or woodland), whereas zoophagous species are most affected by the distance to the next tree (26 %) and the tree diameter (21 %).

The overall number of red-listed species ranged from 2 to 20 per tree and differed significantly between solitary (mean=11.8) and woodland trees (mean=8.6) ( $p < 0.039$ , t-test). This pattern is mainly due to differences in the number of species classified as “vulnerable” under the IUCN criteria (critically endangered  $p < 0.058$ , Wilcoxon rank-sum test; endangered  $p < 0.699$ , t-test; vulnerable  $p < 0.006$ , t-test). The main parameters influencing the number of red-listed saproxylic beetle species were tree diameter (26 %) and the number of tree hollows (17 %). For both parameters we found a positive association with the number of red-listed species.

## **4 Discussion**

We found that saproxylic beetle assemblages are affected by both habitat and fragmentation parameters. Our results show that habitat parameters explain most differences in species richness, as well as the number of specimens, whereas parameters related to fragmentation are only responsible for about 20 % of this variability. This applies to the number of species per oak tree, number of specimens and rarefied species richness.

### ***4.1 Are there any negative effects of fragmentation?***

Habitat fragmentation is generally expected to be of greater significance for habitat specialists than for generalists (Steffan-Dewenter & Tscharntke 2002). Habitat isolation has been found to be important for some insects at larger spatial scales, whereas patch size is more important within the movement range of the studied insect species (Krawchuk & Taylor 2003). Many saproxylic beetles are substrate specialists and Speight (1989) stated that habitat loss and isolation are responsible for a high proportion of endangered species in saproxylic insects. It is widely

accepted that beetles' responses to habitat fragmentation are dependent on specific species' traits, such as wing development, and on the habitat conditions themselves (Driscoll & Weir 2005). Isolation and fragmentation are perhaps a threat for many unwinged species with low dispersal abilities (Assmann 1999; Henle et al. 2004), but a threat can even be observed in full-winged invertebrate species (Thomas 2000). Almost all saproxylic beetle species are winged and are able to fly; time-limited resources such as dead wood require a good power of dispersal. Our results show that saproxylic beetles are affected by fragmentation, but habitat parameters explain much more variability than fragmentation parameters.

Solitary oaks harbour a greater species richness than woodland oaks. In order to determine the respective contribution of habitat configuration and habitat fragmentation we decoupled both effects from each other (cf. Yaacobi et al. 2007 for area and fragmentation). We found that fragmentation parameters contribute on average only 20 % to the variance in species richness and to the number of individuals. This means we have only weak effects on species richness caused by habitat fragmentation. Our study analysed maximum distances of 200 m for single trees to woodland. Individual oaks were at a maximum distance of 100 m from the next oak tree. Schiegg (2000) analysed the impact of dead wood fragmentation and volume on saproxylic beetles in a beech-spruce forest. She observed a relationship between species richness and dead wood connectivity only on the 150 m scale and concluded therefore that for saproxylic beetles habitat fragmentation occurs only on a local scale. A recent study in Australia showed that age effects and differences in structural composition are stronger than pure distance effects when comparing similarity and richness of rainforest beetle communities and restored woodland sites (Grimbacher & Catterall 2007). Despite the fact that they found some specialist species strongly affected by isolation, the impact of fragmentation on insect communities may also be dependent on the spatial pattern of fragmentation, e.g. inter-patch distances (Greze et al. 2004). Müller & Gossner (2007) showed the sensitivity of herbivorous beetles and true bugs living on oaks to habitat isolation; they found no such relationship for saproxylic beetles. Our results show that corticolous beetle species are sensitive to the spatial arrangement of trees, sharing larger proportions of the assemblage on bigger trees and when trees stand close together. We found similar patterns for zoophagous species. Most of the corticolous species in the assemblages we studied are predators (67 % on average). This



suggests that predatory species in particular are affected by spatial fragmentation of tree habitats and were thus found less frequently in the beetle assemblage. However, this would support the trophic rank hypothesis when applied to the species–area or the species–distance relationship (Holt et al. 1999). Trophic structure in insect–plant food webs was found to be influenced by patch area because of edge effects (Valladares et al. 2006). The trophic rank hypothesis claims a stronger relationship for species of a high trophic rank in a given community, e.g. predators. Such species usually have small population sizes or a low abundance for energetic reasons and are therefore more prone to extinction on local patches. Smaller habitat patches (single or few trees) or more isolated habitat patches (solitary trees) can not host a large predator population. In general, zoophagous beetle species show low abundance compared to most lignicolous species. We conclude that predatory saproxylic beetle species are negatively affected by habitat fragmentation because of decreasing habitat area and larger distances between patches.

#### **4.2 Landscape structure does influence habitat quality and assemblage structure**

The solitary oaks studied differ in shape from woodland oaks, because branches begin at a lower level and in most cases solitary trees are smaller than their counterparts in closed stands. Trees in pastures are different in shape and structure from woodland trees (Rackham 1995). Grazing is responsible for the fact that solitary oaks have more sun-exposed tree trunks than their counterparts in woodlands. We also found dead branches (> 10 cm diameter) more frequently on solitary oaks. This suggests that trees with a given distance to others of the same species offer habitat conditions differing from those in closed woodlands. Microhabitats of saproxylic beetles are one example.

These differences may be of importance for species dependent on warm conditions. Many saproxylic beetle species, especially those that are rare in Central Europe, are dependent on warm conditions during their larval development (Bense 1995) that may be favoured by patchy-structured semi-open landscapes or scattered trees. Our results indicate that lignicolous species are affected by the strength of insolation on the oak trunk. A large number of these species are xylophagous species (50 % on average) and feed on the wood itself. We found that these xylophagous species do benefit from the more insolated solitary oaks. This is also true for *Cerambyx cerdo*

(Buse et al. 2007), a longhorn beetle that is suggested to be an ecosystem engineer (Buse et al. 2008). Solitary oaks colonised by *C. cerdo* were again richer in saproxylic beetle species than other oaks. However, the occurrence of *C. cerdo* contributed little when explaining the variability in our dataset. The difference in rarefied species richness between solitary and woodland oaks was much smaller than the differences found between oaks colonised and uncolonised by *C. cerdo* (cf. Buse et al. 2008).

The amount and diversity of dead wood are considered to be among the most influential parameters determining saproxylic beetle species richness (Økland et al. 1996). The most important habitat parameter influencing the number of saproxylic beetle species and the number of red-listed species in our study is the tree diameter, whereas rarefied species richness is affected by the amount of large dead wood on the oaks, trunk insolation and the number of tree hollows. Considering that the amount of large dead wood on the oaks and the number of tree hollows are strongly dependent on the trees' age, this suggests that oak veterans host a maximum of saproxylic beetle diversity (Jonsell et al. 1998; Ranius & Jansson 2000). Several beetle species dependent on specific structures provided by old oaks have been found exclusively in our study, e.g. *Euglenes oculatus* (Aderidae), and the following were found particularly on solitary oaks, e.g. *Euglenes pygmaeus* (Aderidae), and *Oligomerus brunneus* (Anobiidae).

## **5 Conclusion**

On the basis of our results we conclude that fragmentation and isolation of habitat patches play a less important role for overall saproxylic species richness than previously thought. Parameters describing habitat configuration, e.g. tree diameter, for saproxylic beetles are more important. Nevertheless, some habitat and trophic guilds did respond to changes in landscape structure. As overall species richness and the number of endangered species are higher on solitary oaks, we recognize that solitary oaks are of high conservation value. Therefore, fragmentation as discussed here is not a problem but an advantage for nature conservation. A large number of solitary oaks were deliberately planted in the past to serve several purposes, e.g. dike protection in floodplains and for aesthetic reasons in landscape architecture. Thus, nature conservation should pay more attention to recent stands with a large number of solitary oaks. The floodplain landscape of the River Elbe in Germany (Saxony-Anhalt, Lower Saxony) harbours one of the largest numbers of

solitary oaks world-wide and is claimed as a natural and cultural heritage (Krummhaar 2002). The shortage of young solitary trees is problematic because we know that veteran trees in particular often host a maximum of saproxylic beetle diversity. Future conservation efforts should not hesitate to develop parts of existing woodlands into semi-open stands or to plant single young trees as this may be an important means of providing appropriate habitat conditions for saproxylic beetles in the coming decades or centuries.

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**Table 1** Parameters analysed on solitary (n=14) and woodland (n=14) oak trees. Differences between the two groups were tested using the Wilcoxon rank-sum test or, in the case of nominal scaled variables, Fisher's exact test. \*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$

<i>Measured variable</i>	<i>Solitary oaks</i> <i>(no. of cases or mean)</i>	<i>Woodland oaks</i> <i>(no. of cases or mean)</i>	<i>Test for differences</i>
<i>Habitat parameters</i>			
Trunk diameter (dbh <sup>a</sup> )	1.50 m	0.98 m	$p < 0.001$ ***
Tree height	23 m	26 m	$p < 0.018$ **
Height of lowest branch > 5 cm diameter	3 m	4 m	$p < 0.007$ **
Dead branches > 10 cm diameter	18.6 m	11.4 m	$p < 0.031$ *
Trunk hollows with entrance > 5 cm diameter	7 with 0 hollows; 7 with 1 or more hollows;	12 with 0 hollows; 2 with 1 or more hollows	$p < 0.103$ (Fisher's exact test)
Colonisation by <i>Cerambyx cerdo</i> (both old or recent)	5 recent or old colonised; 9 not colonised	all not colonised	$p < 0.042$ *
Trunk insolation	29 % of reference point	13 % of reference point	$p < 0.005$ **
Occurrence of barkless wood	7 with; 7 without	1 with; 13 without	$p < 0.033$ *
Fungi infections	14 with fungi infections	3 with fungi infections; 11 without fungi infections	$p < 0.001$ *** (Fisher's exact test)
<i>Fragmentation parameters</i>			
Distance to next tree	28 m	8 m	$p < 0.001$ ***
Distance to next tree group	66 m	-	-

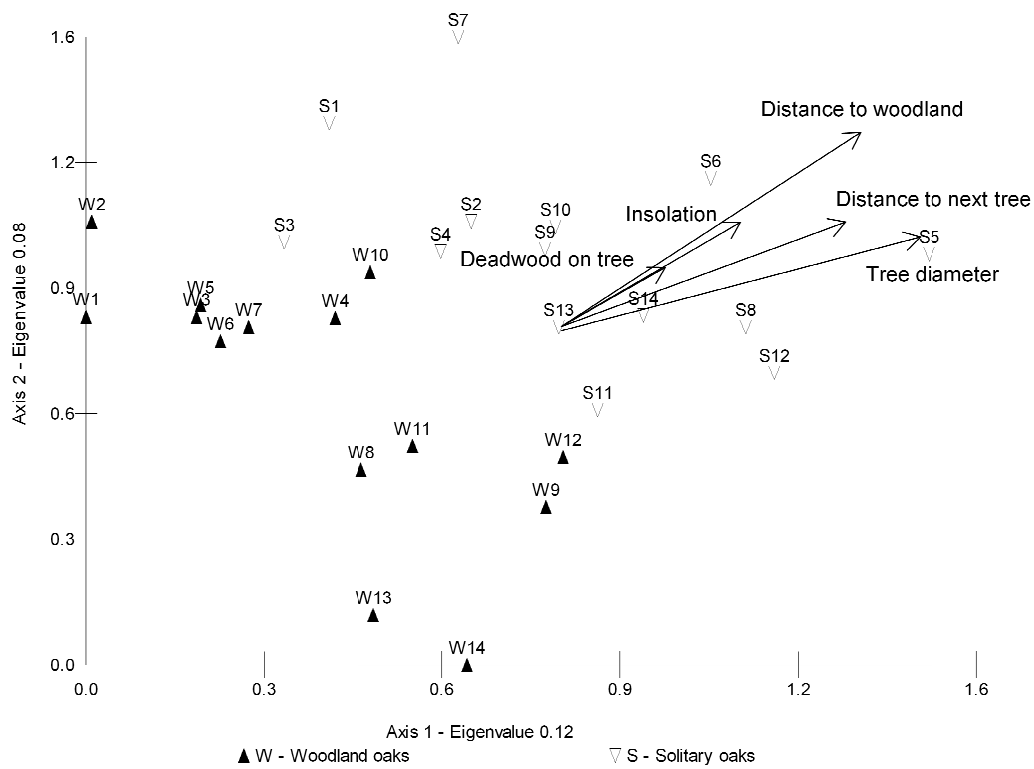
<sup>a</sup> Diameter at breast height

**Table 2** Total independent contribution (in %) of each parameter to the number of species, number of individuals and rarefied species richness per oak tree calculated with a hierarchical partitioning procedure.

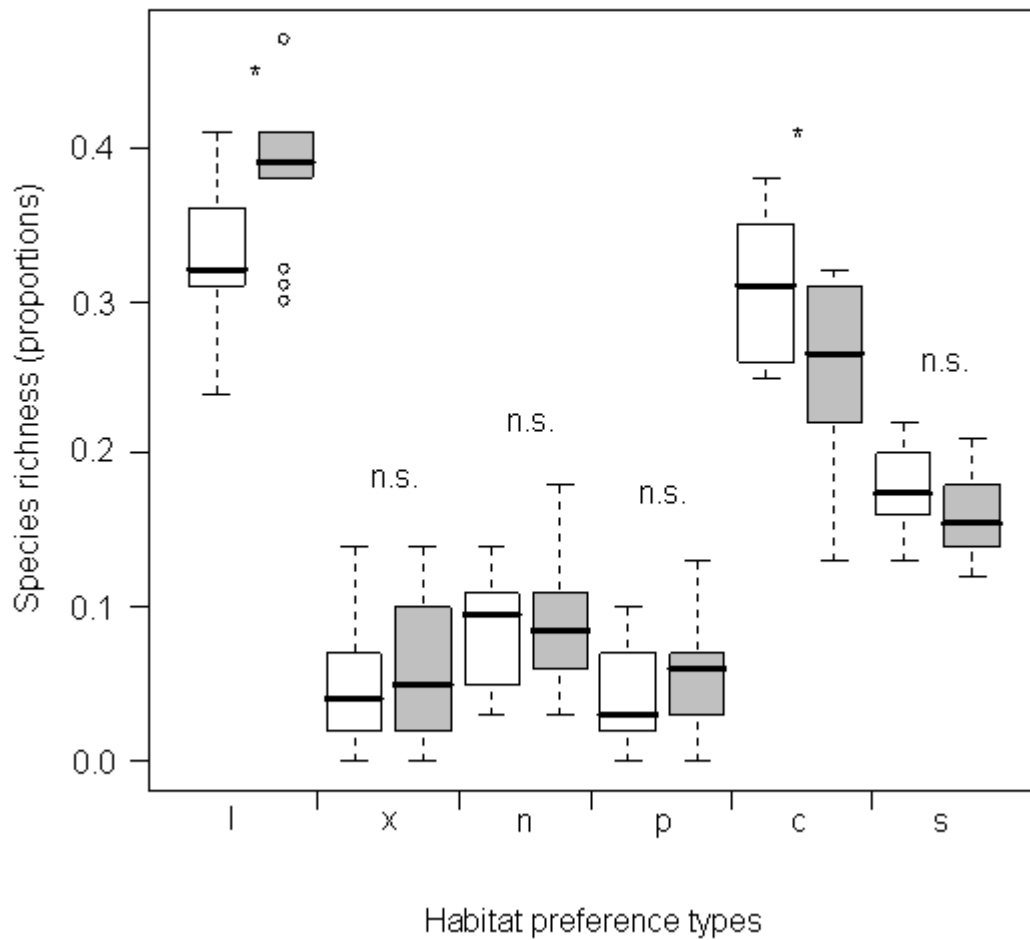
<i>Parameter</i>	<i>Number of species</i>	<i>Number of individuals</i>	<i>Rarefied species richness</i>
<b><i>Ecological parameters</i></b>			
Occurrence of barkless wood	9.33	18.46	7.92
Dead branches > 10 cm diameter	6.70	22.56	10.78
Trunk insolation	8.12	10.23	11.79
Height of lowest branch	5.74	2.94	7.10
Tree height	5.64	4.38	6.83
No. of trunk hollows	14.72	4.62	13.06
Colonisation by <i>Cerambyx cerdo</i>	7.13	5.88	9.11
Trunk diameter	23.02	13.41	9.71
<b><i>Fragmentation parameters</i></b>			
Position in landscape	7.58	4.84	8.79
Distance to next tree	3.18	10.51	7.33
Distance to next tree group	8.83	2.17	7.57
<b>Overall ecological impact</b>	<b>80.4</b>	<b>82.5</b>	<b>76.3</b>
<b>Overall fragmentation impact</b>	<b>19.6</b>	<b>17.2</b>	<b>23.7</b>



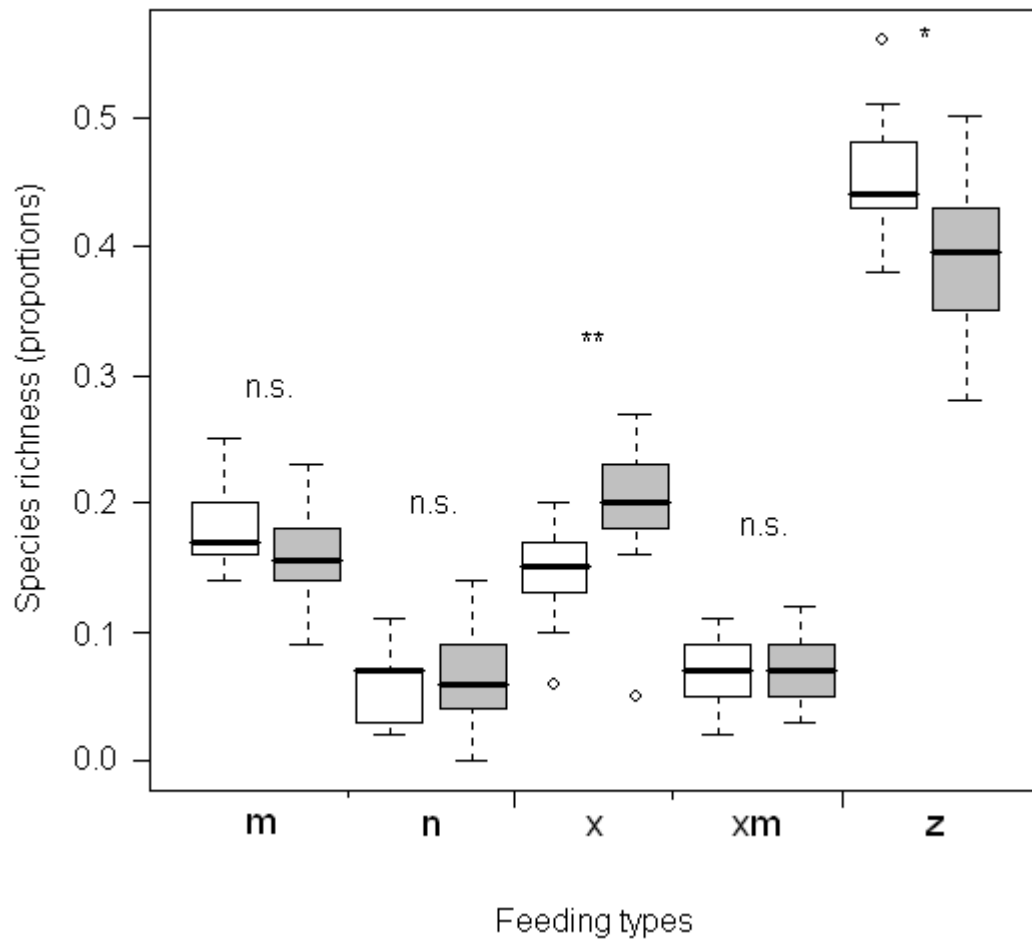
**Figure 1** Detrended correspondence analysis of the 28 samples x 172 species showing plot positions along the two first axes. Filled triangles represent the woodland oaks, and open triangles show the solitary oaks. All four axes explained 31 % of the total variance, whereas the first two axes shown here explained 22 %.



**Figure 2** Proportions of saproxylic beetle species captured on woodland (white bar, n=14) and solitary (grey bar, n=14) oaks and classified into six habitat guilds: l=lignicolous ( $p < 0.018$ ), x=xylodetriticolous ( $p < 0.579$ ); n=nidicolous ( $p < 0.982$ ), p=polyporicolous ( $p < 0.418$ ), c=corticolous ( $p < 0.017$ ), s=succicolous ( $p < 0.128$ ); n.s.=not significant. The horizontal lines show the median, 25 % and 75 % quartiles, and the dashed lines indicate the range of the data.



**Figure 3** Proportions of saproxylic beetle species captured on woodland (white bar, n=14) and solitary (grey bar, n=14) oaks and classified into eight feeding guilds. The figure shows the five most species-rich guilds: m=mycetophagous, n=necrophagous, x=xylophagous, xm=xylomycetophagous, z=zoophagous. Differences were tested using the Wilcoxon rank-sum test: n.s. = not significant; \*  $p < 0.05$ ; \*\*  $p < 0.01$ . The horizontal lines show the median, 25 % and 75 % quartiles, and the dashed lines indicate the range of the data.



# IV

## **Saproxylic beetle assemblages of three managed oak woodlands in the East-Mediterranean**

J. BUSE, B. FELDMANN, T. DAYAN, T. LEVANONY, A. TIMM & T. ASSMANN

(Manuskript)

## Abstract

The Mediterranean basin is considered to be a biodiversity hotspot for both plant and animal taxa. Oak woodlands belong to the natural vegetation in most Mediterranean regions but have suffered from a long history of woodland devastation and overgrazing. The remaining woodlands have been managed in different ways, and we expected this to have had effects on the fauna associated with trees. We investigated three different sites in the East Mediterranean for the impact of woodland management on dead wood and tree structures and the relevance for saproxylic beetle assemblages. Our results show differences in tree diameter, stem density and dead wood diversity between the three sites. Old oaks in the semi-open woodland are characterised by diverse stages of dead wood and harboured most saproxylic species and most individuals. With regard to rarefied species richness we found that the coppice woodland with a high stem density and medium-sized trees has the richest beetle assemblage. Overall species richness was in general strongly associated with the diameter of the oaks. Our findings reveal the importance of old trees in maintaining saproxylic beetle diversity. We discuss the impact of different management options on tree shape and woodland structure, issues which are also important for the saproxylic beetle assemblage associated with Mediterranean oaks. We conclude that oak woodlands in the Near East – and especially those woodlands that have been used and managed in a sustainable way – represent a valuable resource for insect diversity.

**Key words:** *Quercus calliprinos*; Near East; mediterranean; saproxylic; dead wood; woodland structure; biodiversity

## 1 Introduction

Historical documents indicate that woodlands in the Mediterranean basin have been overexploited by man since Roman and Byzantine times, resulting in degraded forms of woodlands and widespread regions cleared of mature woody vegetation (Naveh and Dan 1973, Grove and Rackham 2003). Anthropogenic disturbances such as grazing, fire management and agricultural techniques are the factors which have influenced the external shape and type of these woodlands (Rundel 1998). Traditional land-use with goats, sheep and other livestock meant that it was not

possible for the woodlands to recover until modern economic pressure lowered the number of livestock and thus the grazing pressure on the landscape. Nevertheless, historical paintings indicate the persistence of single trees and groups of trees in pasture landscapes. (e.g. Schuler 1999). Moreover, a few sacred oak trees have survived the hazards of historical land use. The graves of holy men in the shade of these trees furthers the Moslems' belief that a curse will fall on anyone who cuts down the trees; this idea afforded such trees efficient protection for centuries. Thus, both ancient and younger trees have survived in the Israeli landscape (Danin 1989). Due to land-use changes in the last 50 years a natural recovery of the oak woodlands in Mediterranean-type ecosystems of Israel can be observed (cf. Dufour-Drur 2005). The genus *Quercus* dominates this maquis vegetation and is represented in Israel by several native species. Today the evergreen Palestine oak (*Quercus calliprinos*) is the most common tree species of the Israeli Mediterranean region (Shmida 2006). This species, then, would appear to be potentially important for saproxylic insects because of its frequent distribution and its evolutionary significance as a native tree species. It is likely that major parts of the Israeli landscape in the Mediterranean-climate region would consist of oak-dominated woodlands under natural conditions.

Studies from temperate and boreal regions on saproxylic insect diversity have shown a positive relationship between tree diameter and species richness (Jonsell et al. 1998, Ranius and Jansson 2000, Grove 2002). There are two main reasons for increased species richness of beetles in mature and ancient trees: a larger number of microhabitats and the occurrence of specialists dependent on late-successional tree stages, e.g. *Osmoderma eremita*, a European species which lives in tree-hollows (Ranius and Nilsson 1997), *Cerambyx cerdo*, a species predominantly occurring on oaks bigger than 60 cm in diameter (Buse et al. 2007). Different management strategies can also be expected to have a considerable impact on patterns of saproxylic beetle species richness and community structure in Mediterranean woodlands. At present, we have information on how human impact affects plant diversity of woodlands (e.g. Cowling et al. 1996, Schmitz et al. 2007) or birds (e.g. Vallecillo et al. 2008) in Mediterranean regions, but we know very little about how invertebrates respond to different management practices. Grazing either by cattle or goats/sheep and afforestations are considered to be the main human impacts on flora and fauna in the Mediterranean region (Maestre et al. 2003, Henkin et al. 2007,

Alrababah et al. 2007). Studies from Northern and Central Europe have shown the relevance of ecological continuity and forest history for woodland structures that are important determinants of invertebrate richness associated with dead wood (cf. Alexander 1998, Jonsson et al. 2005). However, similar investigations in the Mediterranean are still lacking and ecological research on Mediterranean woodlands is as yet underrepresented (Maranon et al. 1999). For nature conservation strategies and decision making in landscape planning in the Mediterranean it is essential to incorporate basics of dead wood ecology and their associated saproxylic insect fauna. The region with a Mediterranean climate in Israel was particularly strongly affected by the high rates of land consumption in recent decades (Israel Ministry of the Environment 2005). In terms of overall species richness the Mediterranean Basin is considered to be one of the top regions in the world (Médail and Quézel 1999, Myers et al. 2000). The East Mediterranean in particular (e.g. Cyprus, Israel, Lebanon, Syria) shows an enormous diversity of plants and animals compared with other regions in the Mediterranean (Danin 1989). Several saproxylic beetles have been described from the East Mediterranean in recent years (e.g. *Crossotus katbeh* (Cerambycidae), Sama 2000; *Cryphaeus laticeps* (Tenebrionidae), Lillig 2006). Research on occurrence and ecology of these insects is essential to study the distribution of diversity in this region and to develop conservation strategies with a long-term perspective.

The purposes of this paper are (1) to analyse dead wood structures in different managed Mediterranean woodlands, (2) to research saproxylic beetle diversity in this context, (3) to study general patterns of biodiversity and (4) to give recommendations for the conservation of insect diversity in the woodlands of the Near East.

## **2 Material and Methods**

### **2.1 Research area**

We investigated three different plots in the north of Israel to survey the beetle fauna of oaks (*Quercus calliprinos*) under different management conditions. Each plot has been managed in different ways in the past. "Site 1" in the nature reserve "The Fourties" (Carmel Mountains, 32°45'16.5 N, 35°01'44.1 E, 420 m a.s.l.) is characterised by mature old oaks representing a semi-open pasture landscape without any regrowth of juvenile oaks. The other two research plots are located in the Meron Mountains. The second plot "Site 2" is Bar'am Forest (33°02'23.5 N,

35°25'24.3 E, 620 m a.s.l.), a woodland which used to be managed by Christian monks and has been wooded for more than 200 years (cf. Sharon et al. 2001). This woodland is characterised by oaks with several stems from the same root, a result of coppice management in the past. The third plot “Site 3” represents earlier stages of the Mediterranean maquis (33°01'05.5 N, 35°23'19.8 E, 900 m a.s.l.). All plots are grazed either by cattle or by goats and sheep throughout the year. The dominant tree species at all sites is the Palestine oak (*Quercus calliprinos*).

## **2.2 Woodland and tree characteristics**

The richness and abundance of saproxylic beetles may be influenced by a couple of variables. We surveyed our plots for both tree and woodland characteristics. Oaks trees were evaluated for their height and diameter as well as the amount and quality of dead tree parts and the number of holes or cavities in the trunk (Table 1). We counted the number and analysed the quality of fallen dead wood (logs) bigger than 5 cm in diameter on our plots. Thus, we classified the dead wood into three categories, ranging from hard wood with all the bark remaining to soft-decayed wood (cf. Lorenz 2005). We also surveyed the number of dead wood qualities in a 10 m radius around the traps as well as on the tree itself, e.g. fungi infections, snags, freshly broken branches, holes, stumps etc. Finally, we estimated the number of stems per hectare by counting the stems over an area of 50 x 50 metres (0.25 ha) and extrapolating the number to one hectare.

## **2.3 Insect data**

We used flight-interception traps with crossed panels of plexiglass (50 x 30 cm) to survey the flight-active beetle fauna of the woodland plots (see Hyvärinen et al. 2006). In each of the plots, four traps were placed in the canopy of oak trees at a height of 2–4 m above ground level, the exact height being dependent on the shape of the trees. Catches were made from May 16<sup>th</sup> to July 20<sup>th</sup> 2007. We used a mixture employed by Renner (1980) to preserve the catches and we emptied the traps at two-week intervals.

The identification of insects in the Near East is difficult and time consuming because of the lack of identification keys. Thus, individuals were sorted into morphospecies (cf. Oliver and Beattie 1996) and we classified all species at least to family level. The first specimen of each new species encountered was mounted for later comparisons.



All specimens of Staphylinidae, Buprestidae, Elateridae and Tenebrionidae were identified to species level (Table 4). We included individuals from families with a high proportion of species known to be saproxylic (e.g. Palm 1959, Speight 1989), e.g. Cerambycidae or Scolytidae. Specimens from some other families such as Cantharidae or Chrysomelidae have been excluded from this study because their members are not usually dependent on wood. Many rove beetle species in Central Europe are closely related to dead wood structures but we included only such rove beetle species which were known from Europe to be saproxylic. If we had species unknown from Europe, we looked for their genus and included species from genera with saproxylic members.

## **2.4 Statistics**

We calculated analysis of variance (ANOVA) to test for differences between the plots in the characteristics measured. We placed four traps in each plot; therefore the ANOVA uses a four-times replication of the data. Rarefaction was calculated for the number of species grouped for each of the three locations (cf. Krebs 1999). Thus, we were able to compare rarefied species richness for an equal number of 100 specimens per location.

We carried out statistical analyses with R 2.2.0 (R Core Development Team 2005). Rarefaction was performed using the Calculator from John Brzustowski available online (<http://www2.biology.ualberta.ca/jbrzusto/rarefact.php>), which is based on the program RAREFACT.FOR written by Charles J. Krebs.

## **3 Results**

### **3.1 Woodland characteristics**

Tree height and diameter as well as the amount and quality of dead wood on the oaks varied between trees and to a greater extent between plots. In general, the tree individuals from Site 1 harbour much more dead wood in different qualities. The oaks from all plots researched ranged in their diameter from 0.11 to 0.89 metres. Young oaks on Site 3 only had dead branches smaller than 5 cm in diameter (Table 2). None of the surveyed trees on Site 3 showed any large hole or a tree hollow. The oak individuals from Site 1 were extremely rich in different qualities of dead wood. We found they had dead branches thicker than 5 cm with and without bark, some of

them with fungi infections. They usually showed a number of cavities and holes made by some large longhorn beetles (e.g. *Cerambyx*) (Table 2). We found no statistical significant differences in the amount of dead logs between our researched plots. Site 2 in Bar'am Forest has by far the highest density of stems per hectare. There was no significant difference between the amount of dead wood of any kind among the plots. The Site 3 plot is influenced by some young pines scattered between the broadleaved trees.

### **3.2 Diversity of saproxylic beetles in the different managed woodlands**

In total we found 2754 individuals from 99 saproxylic beetle species in the catches made with the 12 flight interception traps. Singletons made up 40 % (40 species) of the total sample.

Recorded beetle species belong to 27 families of Coleoptera. We recorded more species of longhorn beetles (Cerambycidae) than from any other family, but of the individuals caught in the traps the largest number belonged to the family Scolytidae (Table 3). There are significant differences in species richness between our researched plots (Table 2). The highest number of saproxylic species was identified from Site 1, which is characterised by its old tree individuals. Site 2 harboured fewer species than Site 1, but more than the young maquis at Site 3. From Site 1 we identified at least more than double the number of saproxylic beetle species identified from Site 3. In terms of rarefied species richness, Site 2 (Bar'am) harbours the most diverse community of saproxylic beetles. At this site we counted 70 % of the species number reported from Site 1, with only one-third of the number of individuals.

We found 2 morphospecies with more than 2 specimens exclusively at Site 3, 2 species at Site 2 and 17 exclusive species at Site 1. They belonged to several families, most of them within one species. Three longhorn beetle species (Cerambycidae), in particular, were recorded only from the Site 1. When also considering the singletons, we found that more than 50 % of the assemblage from Site 1 are unique species for this location, whereas Site 2 has 36 % and Site 3 only 16 % unique beetle species.

### **3.3 Relationships between tree characteristics and saproxylic beetle assemblages**

The overall raw number of saproxylic beetle species is strongly correlated with the diameter of the investigated oak trees (Fig. 1; Pearson's correlation coefficient  $r=0.861$ ,  $p<0.001$ ). The number of saproxylic beetles species ranged from 9 to 37 per oak tree. The number of individuals caught ranged from 74 to 569 saproxylic beetle specimens per tree and is also strongly correlated with the diameter of the trees (Pearson's correlation coefficient  $r=0.928$ ,  $p<0.001$ ). Tree characteristics such as the amount and diversity of dead wood or the number of cavities are related to tree diameter (Spearman rank or Pearson's correlation coefficient  $r>0.8$ ).

## 4 Discussion

Natural broad-leaved woodlands belong to the group of endangered habitats in the Mediterranean region (Balletto & Casale 1991). However, in spite of their threatened status we do not know much about dead wood and associated diversity in these woodlands.

### ***4.1 Dead wood structures in differently managed Mediterranean woodlands***

The Mediterranean woodlands analysed in this study consist of native tree species and acquired their present shape and structure as a result of extensive human activity. It can be assumed that they differ in their tree architecture and dead wood structure from natural woodlands in this region, because of a variety of different uses by local people; activities such as charcoal production and firewood removal, for example, still influence the trees' shape and therefore woodland structure and are the reason for the scarcity of dead logs and snags in all surveyed woodlands. We found no statistical significant differences between the woodlands observed. One goal of this study was to show the impact of different management options on wood structures and the associated beetle assemblage. We know from historical records that Site 2 in Bar'am used to be managed by monks for firewood and construction timber. By means of selective cutting and coppice management they managed the woodland in a sustainable way, aiming at a long-term preservation of the trees. The results can still be seen today. There are significant differences in the stem density between the woodlands analysed. The largest number of stems per area was observed in the coppice woodland of Bar'am. The even-aged trees are typical for Bar'am, where many stems often grow from the same roots. Similar woodland structures were also common in the past in many European regions (cf. Pott & Hüppe

1991, Rackham 1995, Tack & Hermy 1998). But after traditional woodland management was abandoned in most European regions, the coppice woodlands disappeared. Traditional coppice woodlands are also poor in dead wood. The amount and diversity of dead wood on the oaks differed between the different managed sites we studied. Old oaks in the semi-open stand showed more dead branches and diverse dead wood qualities than the others.

Studies from Europe have shown that unmanaged woodlands accumulate much more dead wood than their managed relatives (Kirby et al. 1998, Jönsson & Jonsson 2007). Comparable studies on dead wood in Mediterranean woodlands are still lacking.

We presumed that the woodland management might have an impact on saproxylic beetle abundance and diversity.

#### ***4.2 Saproxylic beetle richness dependent on site management***

First attempts to analyse saproxylic beetle richness in Mediterranean woodlands were made by Travé (2003) and especially Brin & Brustel (2006). The latter studied saproxylic beetles on cork oaks in Southern France and they found the highest cumulative species richness in a closed cork oak stand with mature trees. We found most species and most individuals on the old oaks in the semi-open woodland, but highest rarefied species richness in the coppice woodland. We thus hypothesised that tree stem density together with the diameter of the oaks is perhaps important for species richness, meaning that at least some of the saproxylic beetle species would benefit from habitat continuity as a result of coppice management over several decades or perhaps centuries. It has been shown that habitat continuity is essential for several European woodland-inhabiting species and taxa (e.g. for lichens: Rose 1976, for plants: Wulf 2004, for ground beetles: Assmann 1999). Taboada et al. (2006) tested Dehesa, mature closed, mature open, young stands for overall ground beetle richness and for indicator species and found no statistical significant differences. However, they showed that the structure of the carabid assemblage is significantly affected by several physical woodland parameters such as tree height and distance between oak trees.

Nevertheless, there is evidence from our findings that many saproxylic beetle species seem to be adapted to old oaks, because we found 17 exclusive species (with 2

specimens and more) on these oak trees larger than 60 cm in diameter. Early stages of the maquis harboured only a portion of the saproxylic species pool in later successional stages and had only few exclusive species. This pattern has also been observed in boreal spruce forests (Økland et al. 1996) and on Swedish oaks (Ranius & Jansson 2000). Although the mature oaks studied here are richer in saproxylic beetles than younger trees, there are perhaps beetle species which prefer young and thinned maquis; for instance, we found *Chlorophorus yachovi* (Cerambycidae) only (3 specimens) on the young maquis oaks.

#### **4.3 Management recommendations for Mediterranean woodlands**

There are many examples which show that grazing increases heterogeneity and establishes a moderate disturbance regime (e.g. Peco et al. 2006, Henkin et al. 2007). Higher levels of spatial and temporal heterogeneity should be related to increasing levels of biodiversity according to a more abundant supply of different niches (e.g. for Mediterranean grasslands: Puerto et al. 1990). This is perhaps also true for Mediterranean woodlands because grazing by cattle or sheep/goats has an impact on tree shape and patch structure and therefore influences woodland heterogeneity. As many saproxylic beetle species are very specific in their habitat requirements, moderate grazing should be continued to maintain a diverse woodland structure with open and shaded habitats.

On the other hand, *Quercus calliprinos* woodlands can be managed through thinning and shrub removal to gain larger and thicker trees (Perevolotsky & Haimov 1992). As we have shown in our study, old oaks harbour more beetle species, and perhaps some late successional species, than younger trees. Therefore, some parts of the Mediterranean woodlands should be managed to allow natural ageing of the oaks. So, selective cutting may be an appropriate management measure for Mediterranean woodlands because it promotes a combination of sustainable use and a high shrub and tree species richness (cf. Torras & Saura, 2008). Traditional coppice management with selective cutting seems to be the most sustainable way to use wood resources and should also contribute to conservation issues. Because coppice management is necessarily a long-term approach to woodland use it includes important ecological features for saproxylic beetles such as habitat continuity, spatial and temporal heterogeneity.

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**Table 1** Surveyed plot characteristics

<b>Measured variables</b>	<b>Categories and units of measurement</b>
<i>Tree level</i>	
Tree height	in metres
Diameter at breast height	in metres
Distance to the next different tree species (oak or pine)	in metres
Occurrence of dead branches on the tree	2 = > 5 cm; 1 = < 5 cm;
Number of cavities or emergence holes (entrance > 1 cm)	
<i>Plot level</i>	
Deadwood amount (diameter in cm x length in metres) in 10 m surroundings (for logs > 5 cm in diameter)	For certain decay classes: 1 – hard wood and all remaining bark 2 – hard wood, partially rotten, log still intact 3 – log well decayed, soft wood
Deadwood amount	Total amount of all decay classes
Deadwood diversity	Number of dead wood qualities within a 10 m radius of the tree and on the tree itself, e.g. fungi infections, snags, fresh broken branches, holes, stumps etc.
Stems (> 10 cm) per hectare	

**Table 2** Differences between maquis, oak woodland and the old oak stand in some parameters; Analysis of variance: n.s. not significant, \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ ;  $\Sigma$ =sum;  $\emptyset$ =mean; SD=Standard deviation.

Parameter	<i>F-value</i>	<i>p</i>	Site 3	Site 2	Site 1
			n=4	n=4	n=4
Number of saproxylic species			$\Sigma=31$ ; $\emptyset$ 14.75	$\Sigma=47$ ; $\emptyset$ 22.00	$\Sigma=75$ ; $\emptyset$ 32.75
Individuals			$\Sigma=493$	$\Sigma=549$	$\Sigma=1712$
Rarefied species richness for 100 individuals			14.69	19.74	17.36
Chao-1 estimation of total species richness (SD)			45.4 ( $\pm 8.77$ )	84.78 ( $\pm 16.44$ )	135.5 ( $\pm 21.92$ )
<b><i>Tree characteristics</i></b>					
Diameter at breast height	57.21	***	$\emptyset$ 0.13	$\emptyset$ 0.28	$\emptyset$ 0.73
Occurrence of dead tree branches	21.82	***	All < 5 cm	$\frac{3}{4}$ > 5 cm	All > 5 cm
Tree height	80.00	***	$\emptyset$ 4	$\emptyset$ 6	$\emptyset$ 8
Number of cavities/holes	12.29	**	$\emptyset$ 0	$\emptyset$ 1.75	$\emptyset$ 67.5
Deadwood diversity	117.91	***	$\emptyset$ 1	$\emptyset$ 2.5	$\emptyset$ 4.25
Distance to other tree species	134.04	***	$\emptyset$ 7.5	$\emptyset$ 100	$\emptyset$ 30
<b><i>Plot characteristics</i></b>					
Amount of dead wood – class 1	1.00	n.s.	$\emptyset$ 0	$\emptyset$ 0	$\emptyset$ 50.25
Amount of dead wood – class 2	2.45	n.s.	$\emptyset$ 0	7.5	0
Amount of dead wood – class 3	1.00	n.s.	$\emptyset$ 0	5.0	0
Amount of dead wood – total	0.81	n.s.	$\emptyset$ 0	$\emptyset$ 12.5	$\emptyset$ 50.25
Stems per hectar	93.05	***	$\emptyset$ 825	$\emptyset$ 2500	$\emptyset$ 160
Fraction of <i>Pinus</i>	18.00	**	~ 10 %	0	0

**Table 3** Species richness and abundance of beetle families sampled in the survey of differently managed oak woodlands.

<b>Family</b>	<b>Number of species</b>	<b>Specimens</b>
Aderidae	1	14
Alleculidae	2	66
Anobiidae	9	90
Anthribidae	1	5
Bostrychidae	1	6
Buprestidae	5	75
Cantharidae	1	1
Cerambycidae	14	24
Cleridae	2	6
Cucujidae	1	1
Curculionidae	1	1
Dermestidae	3	6
Elateridae	5	14
Histeridae	3	5
Laemophloeidae	1	1
Malachidae	5	13
Melandryidae	2	2
Melyridae	7	172
Mordellidae	3	20
Mycetophagidae	2	50
Nitidulidae	4	6
Ptinidae	5	14

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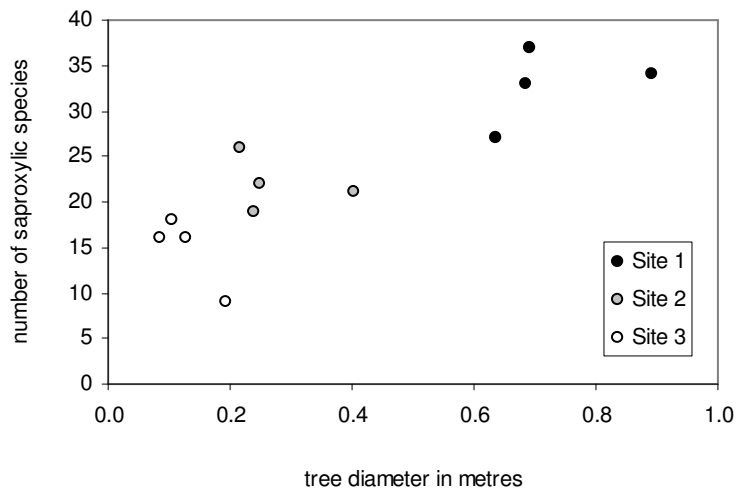
Scarabaeidae	3	35
Scolytidae	8	1960
Serropalpidae	1	1
Staphylinidae	5	156
Tenebrionidae	1	2
Unidentified	3	8

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**Table 4** Identified species from four beetle families. Species names and their catch rates in the three studied plots are given. <sup>1</sup> The status of this species is not clear yet. It is either undescribed (n.sp.) or synonymous (syn.) to *Placusa adscita*. <sup>2</sup> n.sp. undescribed.

Family	Genus	Species	Site 1 (Fourties)	Site 2 (Bar'am)	Site 3 (Maquis)
Buprestidae	<i>Anthaxia</i>	<i>sponsa</i>	.	1	.
Buprestidae	<i>Anthaxia</i>	<i>perrini</i>	9	.	.
Buprestidae	<i>Agrilus</i>	<i>hastulifer</i>	1	.	.
Buprestidae	<i>Agrilus</i>	<i>relegatus</i>	59	1	1
Buprestidae	<i>Agrilus</i>	<i>tenuissimus</i>	2	1	.
Staphylinidae	<i>Hesperus</i>	<i>auricomus</i>	.	1	.
Staphylinidae	<i>Paraphloeostiba</i>	<i>gayndahensis</i>	40	28	39
Staphylinidae	<i>Placusa</i>	<i>adscita</i>	1	12	11
Staphylinidae	<i>Placusa</i>	<i>tachyporoides</i>	1	.	.
Staphylinidae	<i>Placusa</i>	<i>spec.</i> <sup>1</sup>	3	.	20
Elateridae	<i>Cardiophorus</i>	<i>sacratus</i>	1	4	.
Elateridae	<i>Mulsanteus</i>	<i>quillebelli</i>	.	3	.
Elateridae	<i>Melanotus</i>	<i>fusciceps</i>	2	.	.
Elateridae	<i>Adelocera</i>	<i>pygmaea</i>	1	.	.
Elateridae	<i>Melanotus</i>	<i>spec.</i> <sup>2</sup>	3	.	1
Tenebrionidae	<i>Strongylium</i>	<i>saracenum</i>	2	.	.

**Figure 1** Correlation between species richness and the diameter of investigated oak trees. Pearson's correlation coefficient  $r=0.861$ ,  $p<0.001$ . Raw species numbers were used.



## Appendix

Tabelle der in den Jahren 2006 und 2007 nachgewiesenen xylobionten Käferarten. Staphylinidae wurden nur von den Fängen in 2007 bearbeitet.

Family	Genus	Species	RL	Study in 2006 (n=20 oaks)			Study in 2007 (n=28 oaks)		
				Colonisation by <i>Cerambyx cerdo</i>		All	Solitary and woodland oaks		All
				Y	N		S	W	
Aderidae	<i>Anidorus</i>	<i>nigrinus</i>	.	.	.	.	1	.	1
	<i>Aderus</i>	<i>oculatus</i>	2	37	.	37	48	.	48
		<i>pygmaeus</i>	1	3	.	3	25	1	26
Alleculidae	<i>Allecula</i>	<i>morio</i>	3	39	1	40	4	1	5
	<i>Mycetochara</i>	<i>axillaris</i>	2	1	.	1	1	.	1
		<i>linearis</i>	.	68	10	78	85	10	95
	<i>Prionychus</i>	<i>ater</i>	3	6	4	10	2	.	2
	<i>Pseudocistela</i>	<i>ceramboides</i>	2	1	.	1	.	.	.
Anobiidae	<i>Anobium</i>	<i>fulvicorne</i>	.	6	6	12	80	7	87
		<i>nitidum</i>	.	3	1	4	3	1	4
		<i>punctatum</i>	.	.	.	.	.	1	1
	<i>Dorcatoma</i>	<i>chrysomelina</i>	3	7	.	7	16	3	19
		<i>flavicornis</i>	3	15	2	17	27	3	30
	<i>Hedobia</i>	<i>imperialis</i>	.	5	2	7	8	1	9
	<i>Oligomerus</i>	<i>brunneus</i>	3	10	3	13	17	4	21
	<i>Ptilinus</i>	<i>pectinicornis</i>	.	2	1	3	13	.	13
	<i>Stegobium</i>	<i>paniceum</i>	.	1	.	1	.	.	.
	<i>Xestobium</i>	<i>rufovillosum</i>	.	.	2	2	3	2	5
	<i>Xyletinus</i>	<i>pectinatus</i>	3	.	.	.	2	.	2
	<i>Priobium</i>	<i>carpini</i>	.	.	.	.	1	.	1
	Anthribidae	<i>Anthribus</i>	<i>albinus</i>	.	.	1	1	4	4
<i>Phaeochrotes</i>		<i>cinctus</i>	3	.	1	1	.	.	.
<i>Tropideres</i>		<i>albirostris</i>	3	4	1	5	.	.	.
Buprestidae	<i>Agrilus</i>	<i>angustulus</i>	.	1	1	2	.	.	.
		<i>biguttatus</i>	.	.	1	1	.	.	.
		<i>laticornis</i>	.	.	.	.	3	1	4
		<i>olivicolor</i>	.	1	.	1	.	.	.
		<i>sulcicollis</i>	.	11	6	17	4	2	6
Cantharidae	<i>Malthinus</i>	<i>frontalis</i>	.	1	2	3	6	7	13
		<i>fuscus</i>	.	.	.	.	1	.	1
	<i>Malthodes</i>	<i>guttifer</i>	.	.	1	1	.	.	.
		<i>minimus</i>	.	2	.	2	2	2	4
Catopidae	<i>Nemadus</i>	<i>colonooides</i>	.	1	.	1	.	.	
Cerambycidae	<i>Anaesthetis</i>	<i>testacea</i>	3	.	1	1	.	.	.
	<i>Aromia</i>	<i>moschata</i>	.	3	1	4	2	1	3
	<i>Axinopalpis</i>	<i>gracilis</i>	1	.	.	.	2	.	2
	<i>Cerambyx</i>	<i>scopolii</i>	3	4	.	4	8	3	11
	<i>Clytus</i>	<i>arietis</i>	.	1	.	1	.	2	2



		<i>tropicus</i>	2	1	.	1	.	.	.	
<i>Cortodera</i>		<i>humeralis</i>	3	4	3	7	8	.	8	
<i>Grammoptera</i>		<i>abdominalis</i>	.	.	2	2	.	.	.	
		<i>ruficornis</i>	.	.	.	.	.	.	.	
		<i>ustulata</i>	.	1	.	1	.	.	.	
<i>Leiopus</i>		<i>nebulosus</i>	.	2	2	4	.	.	.	
<i>Leptura</i>		<i>quadrifasciata</i>	.	.	.	.	1	.	1	
<i>Mesosa</i>		<i>nebulosa</i>	3	5	7	12	7	3	10	
<i>Pedostrangalia</i>		<i>revestita</i>	2	1	.	1	1	.	1	
<i>Phymatodes</i>		<i>testaceus</i>	.	17	23	40	30	24	54	
<i>Plagionotus</i>		<i>arcuatus</i>	.	.	1	1	.	.	.	
		<i>detritus</i>	2	.	3	3	.	3	3	
<i>Pyrrhidium</i>		<i>sanguineum</i>	.	2	.	2	1	.	1	
<i>Rhagium</i>		<i>mordax</i>	.	3	1	4	3	3	6	
		<i>sycophanta</i>	3	13	2	15	5	7	12	
<i>Stenocorus</i>		<i>quercus</i>	2	1	.	1	.	.	.	
<i>Tetrops</i>		<i>praeustus</i>	.	.	1	1	.	1	1	
		<i>starkii</i>	.	.	.	.	.	1	1	
<i>Xylotrechus</i>		<i>antilope</i>	.	2	1	3	.	.	.	
Cerylonidae	<i>Cerylon</i>	<i>fagi</i>	.	.	1	1	.	.	.	
		<i>ferrugineum</i>	.	2	3	5	.	2	2	
		<i>histeroides</i>	.	5	3	8	1	1	2	
Cisidae	<i>Cis</i>	<i>boleti</i>	.	2	1	3	1	1	2	
		<i>fagi</i>	.	.	.	.	1	.	1	
	<i>Ennearthron</i>		<i>cornutum</i>	.	.	2	2	1	.	1
	<i>Orthocis</i>	<i>alni</i>	.	.	1	1	.	2	2	
		<i>vestitus</i>	.	8	3	11	1	1	2	
Cleridae	<i>Dermestoides</i>		<i>sanguinicollis</i>	1	5	.	5	.	.	
	<i>Korynetes</i>		<i>coeruleus</i>	.	3	.	3	1	.	1
	<i>Opilo</i>		<i>mollis</i>	.	2	4	6	1	1	2
	<i>Thanasimus</i>		<i>formicarius</i>	.	1	.	1	.	2	2
	<i>Tillus</i>		<i>elongatus</i>	3	2	.	2	4	.	4
Colydiidae	<i>Bitoma</i>		<i>crenata</i>	.	1	.	1	.	.	
	<i>Colydium</i>	<i>elongatum</i>	3	1	.	1	.	.	.	
		<i>filiforme</i>	2	10	.	10	1	5	6	
	<i>Pycnomerus</i>		<i>terebrans</i>	1	1	1	2	.	.	
	<i>Synchita</i>		<i>humeralis</i>	.	2	2	4	2	7	9
Corylophidae	<i>Arthrolips</i>		<i>nana</i>	2	1	2	3	.	.	
	<i>Orthoperus</i>		<i>nigrescens</i>	2	.	1	1	.	.	
	<i>Sacium</i>		<i>pusillum</i>	2	.	.	.	2	2	
Cryptophagidae	<i>Cryptophagus</i>	<i>dorsalis</i>	3	1	.	1	.	.	.	
		<i>labilis</i>	2	1	1	2	.	.	.	
		<i>micaceus</i>	2	1	2	3	2	7	9	
		<i>populi</i>	2	1	.	1	.	.	.	
Cucujidae	<i>Pediacus</i>		<i>depressus</i>	.	.	1	1	14	3	17
Curculionidae	<i>Brachytemnus</i>		<i>porcatus</i>	2	2	.	2	1	.	1

	<i>Cossonus</i>	<i>linearis</i>	.	2	.	2	3	3	6
		<i>cylindricus</i>	3	.	.	.	1	.	1
		<i>parallelepipedus</i>	3	.	.	.	1	.	1
	<i>Magdalis</i>	<i>exarata</i>	2	8	8	16	1	2	3
		<i>flavicornis</i>	.	1	1	2	8	1	9
	<i>Phloeophagus</i>	<i>lignarius</i>	.	.	.	.	1	.	1
Dermestidae	<i>Anthrenus</i>	<i>fuscus</i>	.	4	.	4	2	.	2
		<i>goliath</i>	.	1	.	1	.	.	.
		<i>museorum</i>	.	1	.	1	.	.	.
		<i>pimpinellae</i>	.	3	.	3	.	.	.
		<i>scrophulariae</i>	.	4	.	4	1	.	1
	<i>Attagenus</i>	<i>pellio</i>	.	5	4	9	5	3	8
		<i>punctatus</i>	2	7	1	8	3	1	4
		<i>schaefferi</i>	.	.	1	1	.	.	.
		<i>unicolor</i>	.	3	1	4	.	.	.
	<i>Ctesias</i>	<i>serra</i>	.	7	1	8	10	6	16
	<i>Dermestes</i>	<i>lardarius</i>	.	2	.	2	.	.	.
	<i>Globicornis</i>	<i>nigripes</i>	3	70	9	79	47	9	56
	<i>Megatoma</i>	<i>undata</i>	3	6	11	17	7	13	20
	<i>Trinodes</i>	<i>hirtus</i>	3	6	.	6	12	7	19
	<i>Trogoderma</i>	<i>glabrum</i>	.	4	.	4	.	.	.
	Elateridae	<i>Ampedus</i>	<i>balteatus</i>	.	1	.	1	.	.
<i>cardinalis</i>			1	4	.	4	.	.	.
<i>hjorti</i>			2	8	1	9	2	1	3
<i>nigroflavus</i>			3	1	1	2	1	.	1
<i>pomorum</i>			.	2	.	2	1	2	3
<i>quercicola</i>			3	6	1	7	.	2	2
<i>sanguinolentus</i>			.	1	.	1	.	.	.
<i>Brachygonus</i>		<i>megerlei</i>	2	2	.	2	.	.	.
<i>Calambus</i>		<i>bipustulatus</i>	.	.	1	1	4	4	8
<i>Cardiophorus</i>		<i>gramineus</i>	2	4	.	4	2	.	2
<i>Denticollis</i>		<i>linearis</i>	.	.	.	.	1	1	2
<i>Elater</i>		<i>ferrugineus</i>	2	1	1	2	.	1	1
<i>Hypoganus</i>		<i>inunctus</i>	3	2	1	3	2	1	3
<i>Lacon</i>		<i>quercus</i>	1	1	.	1	3	1	4
<i>Melanotus</i>		<i>rufipes</i>	.	6	4	10	1	5	6
<i>Procræus</i>		<i>tibialis</i>	2	10	.	10	.	1	1
<i>Stenagostus</i>	<i>villosus</i>	3	2	2	4	.	.	.	
Endomychidae	<i>Symbiotes</i>	<i>latus</i>	2	.	.	.	1	1	2
Erotylidae	<i>Dacne</i>	<i>bipustulata</i>	.	8	4	12	11	3	14
		<i>collaris</i>	1	.	.	.	1	1	2
	<i>Triplax</i>	<i>russica</i>	.	.	1	1	1	.	1
Eucnemidae	<i>Eucnemis</i>	<i>capucina</i>	3	4	.	4	5	4	9
	<i>Hypocoelus</i>	<i>olexai</i>	3	2	.	2	.	2	2
Histeridae	<i>Paromalus</i>	<i>flavicornis</i>	.	.	.	.	4	3	7
Laemophloeidae	<i>Notolaemus</i>	<i>unifasciatus</i>	2	2	2	4	1	1	2

		<i>castaneus</i>	1	.	1	1	.	.	.	
	<i>Cryptolestes</i>	<i>duplicatus</i>	.	3	2	5	2	1	3	
Lathridiidae	<i>Enicmus</i>	<i>fungicola</i>	.	4	2	6	1	2	3	
		<i>testaceus</i>	2	5	3	8	7	6	13	
	<i>Latridius</i>	<i>hirtus</i>	3	2	1	3	1	1	2	
Leiodidae	<i>Anisotoma</i>	<i>humeralis</i>	.	.	.	.	1	2	3	
Lucanidae	<i>Dorcus</i>	<i>parallelopedus</i>	.	.	1	1	.	1	1	
Lyctidae	<i>Lyctus</i>	<i>linearis</i>	.	1	.	1	.	.	.	
Lymexylonidae	<i>Hylecoetus</i>	<i>dermestoides</i>	.	3	14	17	72	149	221	
		<i>navale</i>	3	8	1	9	1	7	8	
Malachiidae	<i>Malachius</i>	<i>bipustulatus</i>	.	12	10	22	13	7	20	
		<i>flavipes</i>	3	.	.	.	1	.	1	
Melandryidae	<i>Anisoxya</i>	<i>fuscata</i>	3	1	1	2	4	.	4	
		<i>Conopalpus</i>	<i>testaceus</i>	.	7	9	16	2	1	3
		<i>Eustrophus</i>	<i>dermestoides</i>	3	.	.	.	21	2	23
		<i>Orchesia</i>	<i>undulata</i>	.	.	1	1	.	.	.
Melyridae	<i>Dasytes</i>	<i>aeratus</i>	.	.	2	2	1	.	1	
		<i>caeruleus</i>	.	1	5	6	.	.	.	
		<i>flavipes</i>	.	.	2	2	5	19	24	
		<i>plumbeus</i>	.	3	2	5	9	1	10	
		<i>Trichoceble</i>	<i>memnonia</i>	3	2	1	3	2	.	2
Monotomidae	<i>Rhizophagus</i>	<i>bipustulatus</i>	.	9	16	25	17	40	57	
		<i>depressus</i>	.	1	3	4	.	.	.	
		<i>dispar</i>	.	.	.	.	.	4	4	
		<i>parvulus</i>	.	.	.	.	.	2	2	
		<i>picipes</i>	.	2	.	2	.	.	.	
		<i>Cyanostolus</i>	<i>aeneus</i>	3	1	.	1	2	3	5
Mordellidae	<i>Tomoxia</i>	<i>biguttata</i>	.	4	3	7	3	4	7	
		<i>Mordellochroa</i>	<i>abdominalis</i>	.	.	.	.	1	2	3
Mycetophagidae	<i>Litargus</i>	<i>connexus</i>	.	54	166	220	99	448	547	
		<i>balteatus</i>	.	.	.	.	1	.	1	
		<i>piceus</i>	3	3	.	3	8	4	12	
	<i>Mycetophagus</i>	<i>quadripustulatus</i>	.	.	.	.	.	1	1	
		<i>quadriguttatus</i>	.	.	.	.	1	.	1	
Nitidulidae	<i>Cryptarcha</i>	<i>strigata</i>	.	240	187	427	250	390	640	
		<i>undata</i>	.	223	163	386	458	629	1087	
	<i>Epurea</i>	<i>biguttata</i>	.	1	2	3	45	53	98	
		<i>guttata</i>	.	260	96	356	61	49	110	
		<i>unicolor</i>	.	13	13	26	2	6	8	
	<i>Glischrochilus</i>	<i>hortensis</i>	.	35	24	59	9	9	18	
		<i>quadriguttatus</i>	.	13	9	22	5	18	23	
		<i>quadripunctatus</i>	.	2	.	2	3	1	4	
	<i>Soronina</i>	<i>grisea</i>	.	189	100	289	169	99	268	
	<i>Pityophagus</i>	<i>ferrugineus</i>	.	.	.	.	1	.	1	
Platypodidae	<i>Platypus</i>	<i>cylindrus</i>	3	11	1	12	6	15	21	
Ptinidae	<i>Ptinus</i>	<i>rufipes</i>	.	1	.	1	1	.	1	

		<i>sexpunctatus</i>	3	15	8	23	7	3	10	
Pyrochroidae	<i>Schizotus</i>	<i>pectinicornis</i>	.	.	.	.	.	1	1	
Salpingidae	<i>Salpingus</i>	<i>planirostris</i>	.	9	6	15	3	9	12	
		<i>ruficollis</i>	.	.	1	1	1	1	2	
	<i>Vincenzellus</i>	<i>ruficollis</i>	.	.	.	.	19	30	49	
Scaphidiidae	<i>Scaphisoma</i>	<i>agaricinum</i>	.	1	1	2	.	.	.	
Scarabaeidae	<i>Osmoderma</i>	<i>eremita</i>	2	3	1	4	.	.	.	
	<i>Potosia</i>	<i>cuprea</i>	.	2	.	2	.	.	.	
	<i>Valgus</i>	<i>hemipterus</i>	.	2	.	2	.	.	.	
Scolytidae	<i>Dryocoetes</i>	<i>villosus</i>	.	42	4	46	6	3	9	
	<i>Scolytus</i>	<i>intricatus</i>	.	10	19	29	8	3	11	
	<i>Xyleborus</i>	<i>dispar</i>	.	50	24	74	54	171	225	
		<i>dryographus</i>	.	22	6	28	2	1	3	
		<i>monographus</i>	.	339	21	360	208	53	261	
			<i>saxeseni</i>	.	1790	2052	3842	1356	1197	2553
	<i>Xylesandrus</i>	<i>germanus</i>	.	.	.	.	10	60	70	
	<i>Xyloterus</i>	<i>signatus</i>	.	.	.	.	.	1	1	
Scraptiidae	<i>Anaspis</i>	<i>flava</i>	.	30	17	47	51	14	65	
		<i>frontalis</i>	.	2	.	2	3	.	3	
		<i>humeralis</i>	.	2	.	2	2	1	3	
		<i>maculata</i>	.	.	.	.	9	21	30	
		<i>rufilabris</i>	.	2	1	3	4	6	10	
		<i>thoracica</i>	.	4	1	5	16	6	22	
	<i>Scraptia</i>	<i>fuscata</i>	3	13	3	16	14	4	18	
Silvanidae	<i>Silvanus</i>	<i>bidentatus</i>	.	1	1	2	.	2	2	
		<i>unidentatus</i>	.	1	.	1	.	.	.	
	<i>Uleiota</i>	<i>planata</i>	.	2	2	4	.	.	.	
Staphylinidae	<i>Thamiaraea</i>	<i>cinnamomea</i>	3	.	.	.	184	279	463	
		<i>testaceus</i>	.	.	.	.	.	1	1	
	<i>Phloeopora</i>	<i>corticalis</i>	.	.	.	.	3	16	19	
		<i>depressa</i>	.	.	.	.	66	83	149	
	<i>Placusa</i>	<i>tachyporoides</i>	.	.	.	.	32	49	81	
		<i>Velleius</i>	<i>dilatatus</i>	3	.	.	.	8	13	21
	<i>Atheta</i>	<i>euryptera</i>	.	.	.	.	102	116	218	
	<i>Paraphloeostiba</i>	<i>gayndahensis</i>	.	.	.	.	.	1	1	
		<i>lapponica</i>	.	.	.	.	2	4	6	
	<i>Phloeostiba</i>	<i>plana</i>	.	.	.	.	15	51	66	
		<i>Homolota</i>	<i>plana</i>	.	.	.	.	1	1	
	<i>Ischnoglossa</i>	<i>prolixa</i>	.	.	.	.	1	.	1	
	<i>Phloeonomus</i>	<i>pusillus</i>	.	.	.	.	10	4	14	
	<i>Hesperus</i>	<i>rufipennis</i>	2	.	.	.	1	.	1	
	<i>Quedius</i>	<i>scitus</i>	.	.	.	.	.	1	1	
	<i>Philonthus</i>	<i>subuliformis</i>	.	.	.	.	12	15	27	
	<i>Tachinus</i>	<i>bipustulatus</i>	2	.	.	.	.	1	1	
Tenebrionidae	<i>Alphitobius</i>	<i>diaperinus</i>	.	3	.	3	.	.	.	
	<i>Diaperis</i>	<i>boleti</i>	.	1	.	1	.	1	1	

<i>Hypophloeus</i>	<i>bicolor</i>	3	1	.	1	2	1	3
	<i>bicoloroides</i>	1	1	.	1	.	.	.
	<i>fasciatus</i>	2	1	.	1	.	.	.
	<i>unicolor</i>	.	2	1	3	.	.	.
<i>Palorus</i>	<i>depressus</i>	3	15	2	17	.	.	.
<i>Pentaphyllus</i>	<i>testaceus</i>	3	2	.	2	.	1	1
<i>Tenebrio</i>	<i>molitor</i>	.	6	.	6	.	.	.
	<i>opacus</i>	2	.	.	.	.	1	1
<i>Tribolium</i>	<i>castaneum</i>	.	6	2	8	2	.	2
<i>Uloma</i>	<i>culinaris</i>	2	1	.	1	.	.	.
Trogositidae	<i>Nemosoma elongatum</i>	.	.	.	.	1	1	2

## Veröffentlichungen

Die der Dissertation zugrunde liegenden Arbeiten sind mit einem \* gekennzeichnet.

### **Publikationen**

- BUSE, J., RANIUS, T., ASSMANN, T. (2008). An endangered longhorn beetle associated with old oaks and its possible role as an ecosystem engineer. *Conservation Biology* **22**, 329-337.\*
- BUSE, J., SCHRÖDER, B., ASSMANN, T. (2007). Modelling habitat and spatial distribution of an endangered longhorn beetle – A case study for saproxylic insect conservation. *Biological Conservation* **137**, 372-381.\*
- BUSE, J., HÄRDTLE, W. & ASSMANN, T. (eingereicht). The role of habitat fragmentation and habitat configuration for the composition of saproxylic beetle assemblages inhabiting oaks.\*
- BUSE, J., ZABRANSKY, P., ASSMANN, T. (im Druck). The xylobiontic beetle fauna of old oaks colonised by the endangered longhorn beetle *Cerambyx cerdo* (Coleoptera: Cerambycidae). *Mitteilungen der DGAAE* **16**.
- ASSMANN, T., BUSE, J., DREES, C., FRIEDMAN, L., LEVANONY, T., MATERN, A., TIMM, A., WRASE, D. (angenommen). The *Carabus* fauna of Israel – preliminary identification key, faunistics, and habitats (Coleoptera: Carabidae). *ZooKeys*.
- ASSMANN, T., BUSE, J., DREES, C., HABEL, J., HÄRDTLE, W., MATERN, A., VON OHEIMB, G., SCHULDT, A. & WRASE, D.W. (2008). From Latreille to DNA systematics – towards a modern synthesis for carabidology. In : PENEV, L., ERWIN, T. & ASSMANN, T. (eds.). Back to the roots and back to the future? Towards a new synthesis between taxonomic, ecological and biogeographical approaches in carabidology, 41-76.

### **Vorträge**

- BUSE, J. (2008). Sind Solitärbäume artenreicher als Bäume im Bestand? Untersuchungen an Eichen in der Elbtalaue. Faunistisch-ökologische Arbeitsgemeinschaft, Kiel. 20.05.2008.
- BUSE, J. (2008). Zur Bedeutung des Eichenheldbockes und der Baumbestandsstruktur für die an Eichen lebende Käferfauna. Verein für naturwissenschaftliche Heimatforschung zu Hamburg. 29.02.2008.
- BUSE, J., RANIUS, T., ASSMANN, T. (2007). Impact of the endangered longhorn beetle *Cerambyx cerdo* (Coleoptera, Cerambycidae) on the saproxylic beetle assemblage of oak trees. Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sde Boqer (Israel). 05.12.2007

- BUSE, J. (2007). Ecology of saproxylic beetles. Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sde Boqer (Israel). 05.12.2007
- BUSE, J. & T. ASSMANN (2007). Schlüsselarteigenschaften bei einer hochgradig bedrohten Bockkäferart - Zur Frage des 'Ecosystem Engineering' bei holzbewohnenden Insekten. – Entomologentagung 2007, Innsbruck (Austria). 28.02.2007.
- BUSE, J. (2007). Habitatanforderungen und Schlüsselarteigenschaften des Großen Eichenbockes (*Cerambyx cerdo*) in Mitteleuropa. – Ringvorlesung “Aktuelle Entwicklungen im Naturschutz”, Universität Lüneburg. 11.01.2007.
- BUSE, J., SCHRÖDER, B., ASSMANN, T. (2006). A habitat suitability model for the endangered longhorn beetle *Cerambyx cerdo* – ordinal vs. binary response. GfÖ 36<sup>th</sup> Annual Conference, Bremen (Germany). 15.09.2006.
- BUSE, J. (2004). Laufkäfer in historisch jungen und alten Wäldern des Kreises Herzogtum Lauenburg. Verein für naturwissenschaftliche Heimatforschung zu Hamburg. 14.05.2004.
- ASSMANN, T., BUSE, J., DREES, C., EGGERS, J., KRAUSE, H., HÄRDTLE, W., MATERN, A., NOLL, B. & G. VON OHEIMB (2007). Management von Sandheiden in einer sich wandelnden Welt – ökosystemare und carabidologische Untersuchungen – 11. Jahrestagung der GAC, Weißwasser, 23.02.2007.

### **Konferenzbeiträge**

- BUSE, J., SCHRÖDER, B., ASSMANN, T. (2006). A habitat suitability model for the endangered longhorn beetle *Cerambyx cerdo* – ordinal vs. binary response. - Verhandlungen der Gesellschaft für Ökologie 36: 393.
- BUSE, J. and T. ASSMANN (2007). Schlüsselarteigenschaften bei einer hochgradig bedrohten Bockkäferart – Zur Frage des ‚Ecosystem Engineering‘ bei holzbewohnenden Insekten. - Ber. Nat.-med. Verein Innsbruck, Suppl. 17: 31.

### **Posterbeiträge**

- BUSE, J. and T. ASSMANN (2006). A habitat suitability model for the endangered longhorn beetle *Cerambyx cerdo* LINNAEUS, 1758 (Coleoptera, Cerambycidae). ECCB 1<sup>st</sup> European Congress of Conservation Biology , Eger (Hungary).

## Lebenslauf

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### *Persönliche Daten*

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Geburtsdatum 27. November 1979  
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### *Ausbildung*

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2005 – 2008 **Doktorarbeit an der Leuphana Universität Lüneburg**  
Promotionsstipendium der Deutschen Bundesstiftung Umwelt (DBU)  
von 06/2005 – 05/2008

1999 – 2005 **Universität Lüneburg**  
**Umweltwissenschaften** mit den Schwerpunkten **Ökologie** und **Umweltrecht**  
(Diplom in Umweltwissenschaften: Abschlussnote 1.4)

04/2003 - 12/2004 **Diplomarbeit** "Die Laufkäferfauna ausgewählter Waldstandorte unter  
besonderer Berücksichtigung der ökologischen Kontinuität der Standorte  
(Coleoptera, Carabidae)"

1998 – 1999 **Wehrdienst** im PzGrenBat 52 in Rotenburg/Fulda

1992 – 1998 **Städtisches Gymnasium** Mittweida (Allgemeine Hochschulreife, Note 1.9)

1986 – 1992 **Grund- und Realschule** Frankenau

### *Berufliche Tätigkeiten*

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05/2007 – 07/2007 **Forschungsaufenthalt an der Tel Aviv University**, Israel, drei Monate

04/2004 **Praktikum im niedersächsischen Landtag**, Hannover, vier Wochen

10/2001 – 02/2004 **Wissenschaftliche Hilfskraft** im Rechen- und Medienzentrums der Universität  
Lüneburg

08-09/2002 **Praktikum in der Bezirksregierung Lüneburg**, Dezernat für Abfallwirtschaft  
und Immissionsschutz, zwei Monate

08-09/2000 **Praktikum im Nationalpark Bayerischer Wald**, sechs Wochen



### ***Sonstige Tätigkeiten***

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Betreuung von Diplomarbeiten am Institut für Ökologie und Umweltchemie

Studentische Hilfskraft

Mitorganisation und Durchführung einer studentischen Exkursion nach Israel

Exkursionsleitung im Biosphärenreservat Niedersächsische Elbtalaue

### ***Stipendien***

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Promotionsstipendium der Deutschen Bundesstiftung Umwelt (DBU) für drei Jahre

Auslandsstipendium des Deutschen Akademischen Austauschdienstes (DAAD) für drei Monate

### ***Fremdsprachenkenntnisse***

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