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The impact of land-use intensification on pollination and seed-dispersal interactions in the wild cherry (*Prunus avium* L.)

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Dekanin: Prof. Dr. Anna Starzinski-Powitz

1. Gutachterin: Prof. Dr. Katrin Böhning-Gaese

2. Gutachter: Prof. Dr. Ingolf Steffan-Dewenter

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To my mother, who always supported me.

» Perhaps the most important point is to ensure that science never becomes divorced from the basic human feeling of empathy with our fellow beings. «

The Dalai Lama (2005)

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Contents

1 Zusammenfassung der Arbeit

Menschliche Aktivitäten beeinflussen beinahe alle Bereiche des Lebens auf der Erde (MEA 2005a; UNEP 2007). Die Zerstörung und Veränderung natürlicher Lebensräume sind als Hauptursache für den weltweiten Biodiversitätsverlust identifiziert (Harrison and Bruna 1999; Dale et al. 2000; Foley et al. 2005; MEA 2005a). Zusammen mit dem Klimawandel wird die Landnutzungsveränderung daher als einflussreichster Aspekt anthropogen verursachten globalen Wandels betrachtet (MEA 2005a). Landnutzungsveränderung schließt sowohl die Umwandlung natürlicher Habitate in Agrarland oder Siedlungen als auch die Landnutzungsintensivierung in bereits kultivierten Landschaften mit ein. Diese Veränderungen haben weitreichende Konsequenzen für die Artenvielfalt und resultieren häufig in dem Verlust von Arten mit zunehmender Intensität der Landnutzung (Scholes and Biggs 2005).

Biodiversität und Ökosysteme stellen viele verschiedene Funktionen zur Verfügung, wie z. B. die Sauerstoffproduktion, die Reinigung von Wasser und die Bestäubung von Nutzpflanzen. Einige dieser Funktionen sind hilfreich, andere wichtig und wieder andere notwendig für das menschliche Wohlergehen (MEA 2005b; UNEP 2007). Mittlerweile sind Ökosystemfunktionen und die vielen Nutzen, die sie erbringen, zu einem zentralen Thema der interdisziplinären Forschung von Sozialwissenschaften und Naturwissenschaften geworden (Barkmann et al. 2008 und darin enthaltene Referenzen). Dadurch bedingt ist es zu einiger Verwirrung bezüglich der verwendeten Begriffe der „Ökosystemfunktion“ (*engl.* “ecosystem function“) und dem der „Ökosystemdienstleistung“ (*engl.* “ecosystem service”) gekommen (deGroot et al. 2002). Da der Fokus meiner Arbeit auf grundlegenden Funktionen von Ökosystemen liegt, verwende ich im Folgenden den Begriff der Ökosystemfunktion.

Für viele Ökosystemfunktionen ist noch sehr unzureichend bekannt, wie diese von externen Störungen beeinflusst werden (Kremen and Ostfeld 2005; Balvanera et al. 2006). Ökosystemfunktionen werden selten von nur einer einzigen Art aufrechterhalten, sondern meist von einer ganzen Reihe unterschiedlicher taxonomischer Gruppen – alle mit ihren ganz eigenen Ansprüchen. Diese Arten, wie auch deren intra- und interspezifischen Interaktionen, können durchaus unterschiedlich auf die gleiche Störungsquelle oder Störungsintensität reagieren. Dies kann Vorhersagen zum Verhalten von Ökosystemfunktionen extrem erschweren.

Der Zusammenhang zwischen Ökosystemfunktion und den daran beteiligten Arten kann als mathematische Funktion visualisiert werden, indem die Leistung der Ökosystemfunktion gegen die Anzahl der betreffenden Arten aufgetragen wird. Diese Funktionen können sich ganz unterschiedlich verhalten. Es ist wichtig, den Verlauf dieser Funktionen für verschiedene Ökosysteme und deren Ökosystemfunktionen zu kennen, um abschätzen zu können, wie viel Artenverlust in Kauf genommen werden kann, bevor die entsprechende Ökosystemfunktion zusammenbricht. Außerdem kann auf diese Weise festgestellt werden, welche der beteiligten Arten unentbehrlich für die Aufrechterhaltung der Ökosystemfunktion sind oder ob viele redundante Arten die Ökosystemfunktion im Falle eines Artenverlustes stabilisieren können. Sollten Schlüsselarten anfälliger auf Landnutzungsänderung reagieren als weniger „wichtige" Arten, kann ihr Verschwinden schwere Konsequenzen für das Ökosystem haben. Diese Zusammenhänge müssen genau untersucht werden, um qualifizierte Handlungsempfehlungen für den Erhalt bereits betroffener Ökosystemfunktionen geben zu können.

Die Bestäubung und die Samenausbreitung durch Tiere gehören zu den wichtigsten Ökosystemfunktionen und verfügen über ein hohes Potential für Untersuchungen zum Einfluss von Landnutzungsänderungen (Herrera 2002; Sekercioglu 2006). In den temperaten Breiten wird die Bestäubung meist von Insekten übernommen – hauptsächlich Bienen – während in den Tropen viele verschiedene Taxa von Wirbeltieren wie Vögel und Fledermäuse ebenfalls zu dieser wichtigen Funktion beitragen. Neben abiotischen Kräften, die leichte Samen ausbreiten können (z. B. Wind, Wasser, Gravitation), wird die Ausbreitung großer Samen holziger Pflanzenarten meist von hochmobilen Wirbeltiergruppen wie z. B. Vögeln und Säugern übernommen. Diese sind in der Lage, die Samen sowohl über weite Entfernungen als auch sehr zielgerichtet zu transportieren (Schupp 1993; Nathan and Muller-Landau 2000; Herrera 2002; Spiegel and Nathan 2007; Schupp et al. 2010). Beide Ökosystemfunktionen und die wichtigen Dienste, die sie zur Verfügung stellen, sind direkt von Änderungen in der Artenvielfalt betroffen. Für die temperaten Breiten gibt es trotz der großen Bedeutung von Bestäubung und Samenausbreitung nur sehr wenige Studien zu diesem Themengebiet.

In meiner Dissertation untersuche ich schwerpunktmäßig den Einfluss von Landnutzungsänderungen auf Bestäubung und Samenausbreitung. Um die Komplexität der beiden zentralen Ökosystemfunktionen zu reduzieren, habe ich ein vereinfachtes natürliches Modellsystem ausgewählt – den Modellorganismus Wildkirsche (*Prunus avium*) und seine beteiligten Bestäuber und Samenausbreiter. Wildkirschen kommen in verschiedenen Habitaten der modernen Kulturlandschaft vor: vom Wald über strukturell komplexe bis hin zu strukturell einfachen Agrarlandschaften. Die Kombination aus Wildkirsche und der agrargeprägten Landschaftsmatrix in Rheinland-Pfalz sowie die dort vorhandenen Landnutzungsgradienten bieten ein sehr gut geeignetes Modellsystem, in dem gleichzeitig Untersuchungen zur Bestäubung und Samenausbreitung durchgeführt werden können. Dieser Ansatz erlaubt einen direkten Vergleich der Auswirkungen von Landnutzungsintensivierung auf verschiedene Ökosystemfunk-tionen im gleichen System.

Vogeldiversität und Samenausbreitung entlang eines anthropogenen Landnutzungsgradienten: hohe Samenentnahme in strukturell einfachem Agrarland (Chapter 3):

Bisher haben nur wenige Studien den Zusammenhang zwischen Biodiversität und Ökosystemfunktion auf der Landschaftsebene analysiert, obwohl die zugrundeliegenden Zusammenhänge und Mechanismen, die aus den bisherigen experimentellen Studien bekannt sind, in natürlichen Systemen durchaus andere sein könnten. Daher habe ich die Vogeldiversität und die Samenausbreitung bei 38 Wildkirschbäumen (*Prunus avium* L.) quantifiziert, die entlang eines anthropogenen Landnutzungsgradienten von Wald über strukturell diverse bis hin zu strukturell einfachen Agrarsystemen verteilt waren.

Zunächst habe ich im Frühling die Diversität innerhalb der lokalen Vogelgemeinschaft in der Umgebung (70 m Radius) der 38 Wildkirschen bestimmt. Dazu wurden dort die Artenzahl und die Gesamtabundanz aller Vögel während der Brutsaison mit Hilfe von Punkt-Stopp-Zählungen ermittelt. Danach habe ich im Sommer Art und Anzahl der baumbesuchenden Vögel sowie die Anzahl der entnommenen Wildkirschsamen und die daraus resultierende Samenausbreitungsrate bestimmt. Zu diesem Zweck wurden ab Sonnenaufgang an jedem Untersuchungsbaum achtstündige Baumbeobachtungen während der Hauptreifezeit der Wildkirschen durchgeführt. Beim Abflug der beobachteten Vögel vom Untersuchungsbaum wurde zusätzlich versucht, die zurückgelegte Strecke bis zur ersten Landung und das dort vorhandene Mikrohabitat zu dokumentieren. Außerdem wurden für jeden Baum folgende Variablen erhoben, um diese in den folgenden Analysen als Kovariablen zu integrieren: Fruchtverfügbarkeit am Untersuchungsbaum, generelle Fruchtverfügbarkeit in der Umgebung (etwa durch gleichzeitig fruchtende Bäume oder Sträucher), durchschnittliche Größe und Gewicht der Früchte, sowie deren Farbe.

Die Analyse der aufgenommenen Daten zeigte, dass eine hohe Landnutzungsintensität zu niedrigem Artenreichtum und niedrigen Abundanzen innerhalb der lokalen Vogelgemeinschaft um die untersuchten Wildkirschbäume führen kann, was wir nach den Ergebnissen früherer Studien bereits erwartet hatten. Nichtsdestotrotz wurden Bäume in strukturell einfachen Agrarsystemen im Mittel genauso oft besucht wie Bäume in strukturell komplexen Landschaften und naturnahen Wäldern. Außerdem kam es mit steigender Landnutzungsintensivierung zu keiner Abnahme in der Anzahl an Früchten, die durch früchtefressende Vögel vom Baum wegtransportiert wurden. So zeigte sich, dass die zugrundeliegende Ökosystemfunktion trotz einer offenbar reduzierten lokalen Vogelgemeinschaft sehr robust ist. Ein Grund dafür mag sein, dass sich das Bewegungsverhalten der samenausbreitenden Vögel und damit die durch sie zurückgelegten Entfernungen entlang des anthropogenen Landnutzungsgradienten in Anpassung an das Habitat veränderten. Es scheint, dass Vögel in strukturell einfacheren Agrarsystemen längere Strecken bei der Nahrungssuche zurücklegten. Dies legt nahe, dass in Ökosystemen, in denen die Ökosystemfunktion durch hoch mobile Vektoren vermittelt wird, das Bewegungsverhalten und die zurückgelegten Entfernungen eine bedeutende Rolle spielen. Ein Anstieg der zurückgelegten Entfernungen mit zunehmender Landnutzungsintensivierung könnte auch in anderen Systemen, in denen die Ökosystemfunktion von „mobilen Vektoren“ (engl. „mobile links”) abhängig ist, häufig zu finden sein.

Einfluss von Habitatkomplexität und Landschaftskonfiguration auf Bestäubungs- und Samenausbreitungsinteraktionen bei Wildkirschbäumen (Chapter 4):

Eine global voranschreitende Landnutzungsintensivierung ist die Hauptursache für den Rückgang der Artenzahlen in anthropogen beeinflussten Landschaften. Gerade der Verlust funktionell wichtiger Arten kann die Leistung elementarer Ökosystemfunktionen wie z. B. Bestäubung und Samenausbreitung stark herabsetzen. Jedoch ist immer noch umstritten, wie die komplexen Beziehungen zwischen Landnutzungsintensität, Biodiversität und solchen Ökosystemfunktionen miteinander verwoben sind. Daher habe ich die Artenzahlen von Bienen, deren Blütenbesuchsraten und den daraus resultierenden Bestäubungserfolg an 32 Wildkirschbäumen quantifiziert. Diese Untersuchungen erfolgten wieder an Bäumen entlang des zuvor bereits beschriebenen Landnutzungsgradienten von naturnahem Wald bis hin zu intensiv genutztem Agrarland.

Die Auswirkungen von Landnutzungsänderungen wurden auf zwei verschiedenen räumlichen Skalen näher untersucht: a) strukturelle Habitatqualität/Habitatvielfalt (engl. „habitat diversity“) auf kleinräumigem lokalen Maßstab (70 m Radius) und b) den Anteil an verfügbaren für Wildkirschen geeigneten Habitaten auf der großskaligen Landschaftsebene (1.000 und 2.000 m Radius). Interessant war hierbei der Vergleich mit den Ergebnissen aus früheren Untersuchungen am gleichen Modellsystem (s. o.). Die Untersuchung verschiedener, für die erfolgreiche Reproduktion der Wildkirsche nötiger Ökosystemfunktionen mit mehreren funktionellen Gruppen (Samenausbreitung durch Vögel und Säuger; Bestäubung durch Bienen) in der gleichen Landschaft und entlang des gleichen Landnutzungsgradienten sollte zeigen, ob sich Veränderungen der Landschaft in gleicher Weise oder völlig unterschiedlich auf die beteiligten Arten und damit letztendlich auf die Ökosystemfunktionen selbst auswirken.

Analog zu den Methoden der ersten Teilstudie zur Samenausbreitung, habe ich zunächst im Frühling die Diversität innerhalb der lokalen Bestäubergemeinschaft in der Umgebung (20 m Radius) der 32 Untersuchungsbäume bestimmt. Dazu wurden dort die Artenzahl und die Gesamtabundanz aller Bienen während der Blütezeit der Wildkirsche ermittelt. Hierzu wurden die Bestäuber mit Hilfe von sog. Farbschalen gefangen und später taxonomisch bestimmt.

Zusätzlich wurden Gildenzugehörigkeit und Anzahl der blütenbesuchenden Bienen sowie die Blütenbesuchsrate ermittelt. Zu diesem Zweck wurden während der Flugzeiten der Bienen an jedem Untersuchungsbaum im Abstand von zwei Tagen je 30-minütige Baumbeobachtungen innerhalb der Hauptblütezeit der Wildkirschen durchgeführt. Außerdem wurden für jeden Baum folgende Variablen erhoben, um diese in den folgenden Analysen als Kovariablen zu integrieren: Blütenverfügbarkeit am Untersuchungsbaum sowie generelle Blütenverfügbarkeit in der Umgebung (etwa durch gleichzeitig blühende Bäume, Sträucher oder krautige Pflanzen). Um schließlich den Bestäubungserfolg beurteilen zu können, wurden während der Blüte an allen Bäumen gleich große Blütenaggregate markiert und vier Wochen später der Anteil an erfolgreich bestäubten Blüten ermittelt.

Bei der Auswertung der gewonnenen Daten zeigte sich, dass der Artenreichtum bei Bienen und die Blütenbesuchsraten in strukturell einfachen Habitaten am höchsten waren, während die Artenzahlen bei Vögeln in strukturell komplexen Habitaten am höchsten waren, nicht jedoch deren Besuchsraten an fruchtenden Bäumen. Die Besuchsraten durch Säuger reagierten hingegen lediglich auf der großräumigen Landschaftsebene. Diese Ergebnisse zeigen deutlich, dass verschiedene funktionelle Tiergruppen unterschiedlich auf Gradienten in Habitat- und Landschaftsstruktur reagieren. Trotz des starken Einflusses auf Bienen und Vögel zeigten die zugehörigen Ökosystemfunktionen Bestäubung und Samenausbreitung keine unterschiedlichen Reaktionen entlang des gesamten Landnutzungsgradienten auf beiden räumlichen Skalen. Dieses Ergebnis legt nahe, dass sich mobile Organismen wie Bienen und Vögel in intensiv genutzten Landschaften über größere Entfernungen bewegen und dabei die Interaktionen der Bestäubung und der Samenausbreitung puffern. Daraus ist zu schließen, dass es nicht ausreicht, lediglich Artenreichtum und die Frequenzen der Interaktion (Besuchsraten) zu quantifizieren, um die letztendlichen Konsequenzen der Landnutzungsintensivierung auf Ökosystemfunktionen (engl. „ecosystem functions“) zu verstehen.

Kürzere Samenausbreitungsdistanzen verringern den Rekrutierungserfolg von vogelausgebreiteten Kirschbäumen in der Agrarlandschaft (Chapter 5):

Innerhalb der durch den Menschen geprägten Landschaften Zentraleuropas sind die verbliebenen Pflanzenpopulationen sehr lückenhaft/ungleichmäßig verteilt, da diese Landschaften aus einem Flickenteppich von sporadisch verteilten seminatürlichen Habitaten bestehen. Um von einer Population zur anderen zu wandern, sind viele holzige Pflanzenarten von tierischen Vektoren abhängig. Zur Untersuchung der qualitativen Leistungen dieser tierischen Vektoren in solchen fragmentierten Landschaften habe ich das Bewegungsverhalten einer häufigen samenausbreitenden Vogelart in naturnahen Landschaften mit dem in agrargeprägten Landschaften verglichen. Anschließend habe ich überprüft, ob Unterschiede im Bewegungsverhalten der Ausbreiter die Rekrutierung von Keimlingen beeinflussen.

Exemplarisch habe ich die Ökosystemfunktion der Samenausbreitung durch früchtefressende Vögel bei der Wildkirsche untersucht. Nach der ersten Studie (s. o.) konnte die Europäische Amsel (*Turdus merula* L.) als eine der Hauptausbreiterarten von Wildkirschsamen identifiziert werden. Daher habe ich beschlossen, die Untersuchungen am Amsel-Wildkirsch-Modellsystem durchzuführen. Besonders vorteilhaft war der Umstand, dass sowohl Wildkirsche als auch Amsel über den gesamten Gradienten anthropogener Landnutzung vorkommen.

Zunächst habe ich Fütterungsversuche mit Wildkirschen (*Prunus avium*) an wild-lebenden Amseln durchgeführt, um die Hervorwürgezeiten für die Samen der geschluckten Früchte zu ermitteln. Im Anschluss habe ich 32 männliche Amseln gefangen, mit Sendern ausgestattet und telemetriert, um den Bewegungen dieser Individuen im Wald und der Agarlandschaft zu folgen. Durch Kombination der Dichteverteilung der Hervorwürgezeiten aus den Fütterungsversuchen und der Bewegungsdaten der Amselindividuen habe ich anschließend die virtuelle Bewegung von Kirschsamen in der Landschaft simuliert. So konnte ich schließlich für Wald- und Feld-Amseln die bei der Samenausbreitung zurückgelegten Entfernungen sowie für jeden Samen den Ort der Ablage bestimmen.

Die Ergebnisse der Simulationen zeigten, dass in der Agarlandschaft mit einem Anteil von 20,8 % mehr Kirschsamen direkt unter dem Mutterbaum landeten als im Wald (Anteil von 9,5

%); in beiden Fällen erfolgte hier also keine echte Ausbreitung. Überraschenderweise waren die mittleren Ausbreitungsdistanzen in der Agrarlandschaft mit 50,8 m deutlich niedriger als im Wald mit 68,2 m. Ebenso verhielt es sich mit der Ausbreitung der Samen über längere Distanzen (engl. „long-distance dispersal“; Distanzen > 100 m). Hier lag der Anteil an weit ausgebreiteten Samen mit 14,9 % in der Agrarlandschaft deutlich unter dem im Wald, wo der Anteil bei 28,2 % lag.

Waldbewohnende Amseln breiteten mit einem Anteil von 98,7 % fast alle Kirschsamen in für Wildkirschen geeignete Habitate aus, während Amseln, die in der Agrarlandschaft leben, mit 85,4 % einen deutlich niedrigeren Anteil in geeignete Habitate transportierten. Da nur hier die Samen der Wildkirsche auch potentiell keimen können, ist nur dieser Anteil der ausgebreiteten Samen für die Wildkirschbäume tatsächlich von Nutzen. Dennoch war der Anteil an nutzbringend ausgebreiteten Samen in beiden Habitattypen deutlich höher als nach den zugrundeliegenden Anteilen an verfügbarem geeignetem Habitat innerhalb der Streifgebiete der Amseln zu erwarten war. Dieser Umstand spricht für eine zielgerichtete Ausbreitung (engl. „directed dispersal“) der Kirschsamen.

Um zu testen, ob die Qualität der Samenausbreitung, also die Entfernung vom Mutterbaum und die Eignung des Habitats am Ort der Ablage der Samen, die Rekrutierung der Keimlinge beeinflusst, wurden sowohl die Dichten der Keimlinge in Agrarland- und Waldpopulationen erfasst als auch die Überlebenswahrscheinlichkeiten einjähriger Keimlinge für beide Habitattypen bestimmt. Die Keimlingsetablierung und die Überlebensraten waren dabei in der Agrarlandschaft deutlich niedriger als im Wald.

Mit den Ergebnissen konnte ich damit erstmals zeigen, dass sich Verhaltensunterschiede von tierischen Samenausbreitern direkt auf die Populationsdynamik von Pflanzen übertragen können und diese damit verändern. Trotz der Tatsache, dass innerhalb der Agrarlandschaft nur verhältnismäßig wenige Samen der Wildkirsche in ungeeignete Habitate ausgebreitet werden, sind die Populationen der Wildkirsche hier anfälliger für ein lokales Aussterben, weil kurze Samenausbreitungsdistanzen letztendlich zu einem schlechten Erfolg bei der Rekrutierung führen.

Schlussfolgerung

Um letztendlich die Auswirkungen von Landnutzungsveränderungen auf die pflanzliche Reproduktion und die Ausbreitung von Pflanzen abschätzen zu können, ist es notwendig, dass alle beteiligten Ökosystemfunktionen in die dazu durchgeführten Untersuchungen mit eingeschlossen werden – also konkret Bestäubung und Samenausbreitung. Die Komplexität von Ökosystemfunktionen wird deutlich, wenn man sich die Bandbreite der Reaktionen der verschiedenen beteiligten Arten auf Landnutzungsintensivierung anschaut. Entlang eines Habitatgradienten auf einer kleinen und einer großen räumlichen Skala sind die Besuchsraten an Kirschbäumen durch Bienen, Säuger und Vögel entweder zurückgegangen, angestiegen oder konstant geblieben, und zwar abhängig vom jeweils betrachteten Taxon. Während Bienen hauptsächlich auf kleinräumige Veränderungen in der Umgebung reagieren, sind Vögel und Säuger eher von Veränderungen auf der Landschaftsebene betroffen. Demzufolge ist die Form der Kurve der zugrundeliegenden Ökosystemfunktion die Summe vieler individueller Kurven verschiedener taxonomischer Gruppen. Wenn also ein Zusammenhang für eine Ökosystemfunktion gefunden ist, kann dieser nicht notwendigerweise generalisiert und auf die gleiche Ökosystemfunktion innerhalb eines anderen Ökosystems übertragen werden oder gar auf eine andere Ökosystemfunktion innerhalb der gleichen Landschaft. Auch könnten wichtige Schlüsselarten stärker auf Landnutzungsintensivierung und auf einer anderen räumlichen Skala reagieren als Arten, die lediglich eine untergeordnete Rolle für die Aufrechterhaltung einer Ökosystemfunktion spielen. Diese Ergebnisse zeigen die Bedeutung von möglichst umfassenden Studien, die so viele Informationen wie möglich über die involvierten Arten integrieren und viele unterschiedliche Methoden und Techniken nutzen. Untersuchungen, die lediglich ausgewählte Bereiche einer Ökosystemfunktion beleuchten, könnten zu Ergebnissen gelangen, die möglicherweise nicht die wahren Auswirkungen von Landnutzungsintensivierung auf Ökosystemfunktionen widerspiegeln.

Im Modellsystem der Wildkirsche waren weder der Bestäubungserfolg noch die Samenausbreitung letztlich von der Intensität der Landnutzung auf irgendeiner der untersuchten räumlichen Skalen beeinflusst. Dies legt nahe, dass Veränderungen in den räumlichen Bewegungsmustern hoch mobiler taxonomischer Gruppen durchaus dazu beitragen können, die Prozesse bei der Bestäubung und der Samenausbreitung gegenüber Landnutzungsintensivierung abzupuffern. Daher ist es nicht nur wichtig wie die Landschaft beschaffen ist, sondern auch wie diejenigen Arten, die zu den jeweiligen Ökosystemfunktionen beitragen, sich durch die Landschaft bewegen. Hoch mobile Arten könnten in der Lage sein, sich von einer naturnahen Struktur zur anderen zu bewegen, so dass sie dabei die Ökosystemfunktion bis zu einem gewissen Grad der landschaftlichen Verarmung stabilisieren. Die vorliegende Arbeit zeigt deutlich, dass es nicht ausreichend ist, Artenvielfalt oder die Frequenz der Interaktionen von Bestäubern oder Samenausbreitern zu messen, um die letztendlichen Konsequenzen für Ökosystemfunktionen zu verstehen. Zukünftige Untersuchungen, die sich mit der Quantifizierung der Auswirkungen von menschlichen Einflüssen auf Ökosystemfunktionen befassen, sollten daher zusätzlich Verhaltensunterschiede von Bestäuber- und Samenausbreiterarten und deren Verhalten auf menschliche Störung betrachten. Innerhalb des Wildkirsche-Amsel-Systems konnte eine detailierte Analyse der Bewegungsmuster der Hauptausbreiterart in Wald- und Feldhabitaten am Ende einen negativen Einfluss von Landnutzungsintensivierung auf die Keimlingsrekrutierung bei Wildkirschen offenlegen, obwohl Bestäubung und Samenausbreitungsraten zunächst unbeeinflusst waren. Letztlich konnte ich so herausfinden, dass Pflanzenpopulationen in der Agrarlandschaft langfristig deutlich gefährdeter sind, lokal auszusterben.

Zukünftige Forschungsprojekte sollten möglichst versuchen, verschiedene Ökosystemfunktionen und an deren Aufrechterhaltung beteiligte Arten innerhalb der gleichen Landschaft in ihre Untersuchungen miteinzuschließen. Ferner ist es notwendig, solche Studien in unterschiedlichen Ökosystemen wie den temperaten Breiten, den Subtropen und den Tropen durchzuführen, da sich die Ergebnisse für bestimmte Ökosysteme nicht ohne Weiteres auf andere übertragen lassen. Besonders wichtig ist es, mehr in Untersuchungen von bereits durch den Menschen veränderte Landschaften zu investieren, da eine wachsende Weltbevölkerung langfristig dazu führen wird, dass diese Kulturlandschaften zur vorherrschenden Landschaftsform werden. Aus diesem Grund benötigen wir dringend mehr Informationen darüber, wie sich zukünftig Agrarlandschaften so gestalten lassen, dass wichtige Ökosystemfunktionen wie

Bestäubung und Samenausbreitung weiterhin durch die beteiligten Arten aufrecht erhalten werden können. Gerade in Zeiten des globalen Klimawandels werden Untersuchungen in diesem Bereich immer wichtiger, da Pflanzen immer schneller ihrer klimatischen Nische folgen müssen. Wie gut dies gelingen kann, hängt von der durch die tierischen Vektoren zur Verfügung gestellten Quantität und Qualität der Bestäubung und Samenausbreitung ab.

2 General Introduction

2.1 Global change and ecosystem functions

Human activities affect virtually all domains of life on a global scale while changing the face of the earth's surface (MEA 2005; UNEP). The destruction and modification of natural habitats at the scale of landscapes has been identified as main cause for the worldwide loss of biodiversity (Harrison and Bruna 1999; Dale et al. 2000; Foley et al. 2005; MEA 2005a). Hence, together with climate change, land-use change is considered the most significant driver of anthropogenic global change (MEA 2005a); this includes the transformation of natural habitats into cropland or settlements as well as the intensification of land-use in already cultivated landscapes.These changes have far-reaching consequences for biodiversity and usually result in the loss of species when land-use intensity increases (Scholes and Biggs 2005).

Biodiversity and ecosystems perform many different functions like oxygen production, purification of water and the pollination of crop plants. Some are useful, others are important and yet others are even essential for human well-being (MEA 2005b; UNEP 2007). For example, pollination has an estimated global value for agriculture alone of around 200 billion US dollars per year (Kearns et al. 1998). Ecosystem functions and the many benefits they provide for humanity have become a central point of interest at the transition of social and natural sciences (Barkmann et al. 2008 and references herein). The lack of clear definitions for the terminology used in this field has resulted in different scientific disciplines and even different authors within one discipline using the same terminology but with different and often contradictory meanings (deGroot et al. 2002). Hence, some confusion exists about the usage of the terms “ecosystem function” (*ger.* “ökosystemare Funktion” or “Ökosystemfunktion”) and “ecosystem service” (*ger.* “Ökosystemdienstleistung“ or “ökosystemare Dienstleistung“). Ecologists usually refer to ecosystem functions when talking about basic biological processes that contribute to the attributes of an ecosystem and which are necessary to maintain an ecosystem. Since my thesis investigates the effects of changes in landscape configuration on the underlying functions of ecosystems and not the beneficial effects of ecosystems, I will only refer to ecosystem services in the following.

For many ecosystem functions it is still poorly understood how they are affected by (external) disturbance (Kremen and Ostfeld 2005; Balvanera et al. 2006). Ecosystem functions are rarely maintained by a single species, but often by a host of species from different taxonomic groups – all with their own specific requirements and needs. These species as well as their interactions with each other are likely to respond differently to the same source and level of disturbance and thus predictions for the response of the ecosystem function can be further complicated. The relationship between ecosystem functioning and contributing species can be visualised when ecosystem functioning is plotted against species richness (see Fig. 2.1).

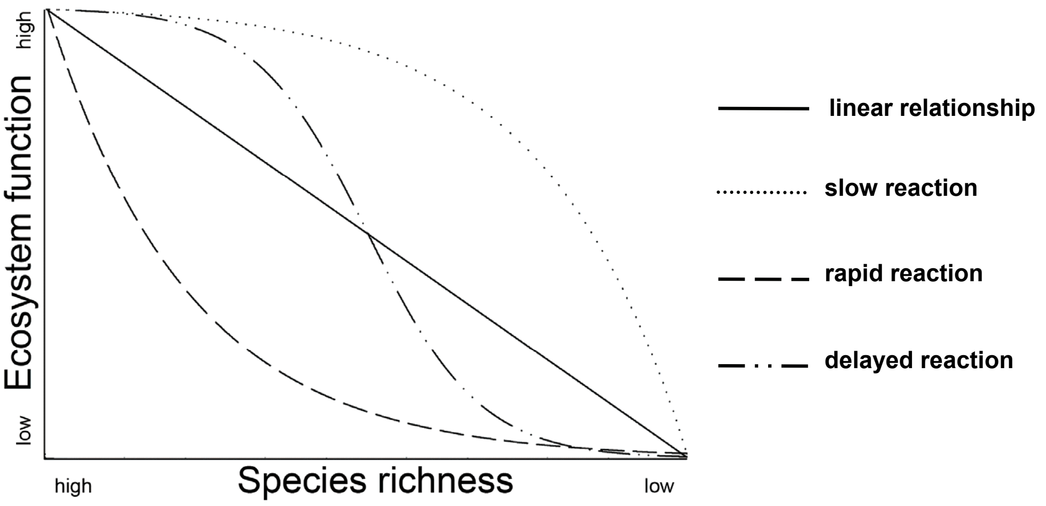

Figure 2.1: Potential relationships between biodiversity (measured as species richness) and ecosystem functioning. [modified after Larsen et al. 2006]

Various relationships between biodiversity (i.e. species richness) and ecosystem functioning are possible. The relationship could be linear when the loss of ecosystem function per species lost is the same across all species richness levels (Fig. 2.1, *solid line*). Mechanisms such as density compensation could result in a rather slow response, because the ecosystem function is more robust against initial species losses and the system is only slowly degraded (Fig. 2.1, *dotted line*). In systems where the ecosystem function is maintained by only one or a few key species an immediate loss of species could lead to a rapid loss of function (Fig. 2.1, *dashed line*). Effects like density compensation or the presence of a redundant set of contributing species may stabilise an ecosystem function resulting in a delayed response; the initial species decline is stabilised up to a certain threshold at which a continuing loss of species results in a sudden and rapid loss of function (Fig. 2.1, *dashed-dotted line*). It is extremely important to identify the shape of the curve for this relationship for different ecosystems and their ecosystem functions in order to assess how much species loss can be tolerated before an ecosystem function will collapse. Even more important, the examples of the possible reactions of ecosystem functions to species loss also illustrate that not species richness alone is influencing the shape of the function, but that it is also important to know which species contribute most and whether redundant species may stabilise the function or not. If key species are more sensitive to land-use change than less important species their disappearance could have severe consequences. This knowledge is therefore needed in order to make the right decisions for conservation activities that aim to stabilise already affected ecosystem functions.

Pollination and seed dispersal by animals are among the most important ecosystem functions (Herrera 2002; Sekercioglu 2006). In temperate regions, pollination is usually provided by insects, i.e. mainly by bees, whereas in the tropics many different vertebrate taxa such as birds (e.g. hummingbirds, sunbirds) and bats (nectar-feeding bats) also contribute to this important function. Apart from abiotic forces that can disperse light-weight seeds (e.g. wind, water, gravity), seed dispersal of large-seeded woody plant species is mostly provided by highly mobile vertebrate taxa such as birds and mammals, which are capable of dispersing seeds directed and over long distances (Schupp 1993; Nathan and Muller-Landau 2000; Herrera 2002; Spiegel and Nathan 2007; Schupp et al. 2010). Both ecosystem functions and the important services they provide will be directly affected by changes in biodiversity. Investigations studying these aspects are still lacking for temperate ecosystems.

In this thesis I investigated how pollination and seed dispersal react to land-use change. To reduce the scale and complexity of the two examined ecosystem functions I focused on a simplified real-world model system. I studied the effects of land-use intensification on the two ecosystem functions of pollination and seed dispersal and the contributing species using the wild cherry (*Prunus avium* L.) as a model organism. Wild cherries occur in all habitat types of modern temperate landscapes from closed forest to structurally complex and simple agricultural landscapes. The combination of the wild cherry and the agricultural landscape matrix of Rhineland-Palatinate in Central Germany with the herein present land-use gradient translate into a highly suitable model system, since the studies on pollination and seed dispersal can be conducted using the same model system. This approach allows for a direct comparison of the effect of land-use intensification on different ecosystem functions in one system.

2.2 Aim and Structure of the Thesis

This thesis aims to extend our knowledge about the effects of land-use intensification on biodiversity and the resulting consequences for the ecosystem functions pollination and seed dispersal by using the wild cherry (*Prunus avium* L.) as a model system. I conducted my study in the temperate agricultural landscape of Rhineland-Palatinate in Central Germany. A combination of different methods from tree observations and species counts up to VHF radio telemetry allowed a comprehensive investigation.

My thesis consists of three major chapters (chapters 3–5) which have been prepared in the form of independent journal publications with its classic style of a short *Abstract*, followed by the respective sections *Introduction*, *Material and methods*, *Results*, *Discussion*, *Conclusion* and *Acknoledgements*. The main research chapters are followed by the *General Conclusions* that integrate the insights of the previous three research chapters. References and Additional Supplementary Material of the three chapters are combined in a shared *Reference* and *Appendix* section at the end of the thesis.

In chapter three, I investigated the effect of land-use intensification on local disperser species richness and abundance and the consequences for seed removal in *P. avium*. I used bird counts and tree observations in combination with GIS maps of land-use to determine how local disperser species are affected by land-use and how that finally affects the removal of cherry seeds. This chapter builds partly upon my joint diploma thesis together with Irina Laube, where both of us collected field data and conducted statistical analyses. In addition, I have recorded data from a second field season with the help of three undergraduate students. I have integrated field data from the two years, conducted all GIS analyses, calculated refined statistical analyses and wrote the manuscript. Irina Laube, Ingolf Steffan-Dewenter and Katrin Böhning-Gaese contributed to study design and manuscript writing.

In chapter four, I focused on pollination and its response to land-use intensification. After measuring species richness and abundance of the local pollinator community under different land-use intensities, I compared the results with data on seed removal by birds from chapter two and with seed removal by mammals. This chapter builds partly upon the diploma thesis of Svenja Tillmann, who recorded field data in the first year, determined bee specimens of the two years and conducted a preliminary analysis in her thesis. For the comparative approach in this chapter, I also included field data on mammalian seed dispersal provided by Claudia Grünewald from her diploma thesis and a resulting publication (Grünewald et al. 2010). I integrated data from the bird (see chapter 3), bee and mammal studies, conducted all GIS analyses, calculated new statistical tests, interpreted the analysis and wrote the manuscript. Svenja Tillmann, Claudia Grünewald, Irina Laube, Matthias Schleuning, Ingolf Steffan-Dewenter and Katrin Böhning-Gaese contributed to study design and manuscript writing.

In chapter five, I used my knowledge about the model system of the wild cherry to take one step further towards understanding how the effects of land-use intensification on seed dispersal affect plant recruitment. To do so, I combined the results of feeding trials for wild blackbirds (*Turdus merula* L.) with blackbird telemetry data to trace the movement paths of cherry seeds through the human-modified landscape. Finally, I incorporated information about seedling recruitment in forest and farmland habitats measured as seedling density and survival rate. Thus, I was able to investigate seed-dispersal distance, directedness of seed dispersal and seedling recruitment. For this chapter, I have collected field data with the help of nine undergraduate students. I was fully responsible for the study design of the telemetry study and conducted the feeding experiments with the captured blackbirds. Irina Laube and Mathias Templin supported feeding experiments. Christoph Böhm and Matthias Schleuning contributed field data and statistical analyses for seedling recruitment of wild cherry trees (data from Staatsexamensarbeit of Christoph Böhm). I conducted all GIS analyses, simulation models, statistical analyses and wrote the manuscript. Irina Laube, Katrin Böhning-Gaese and Matthias Schleuning contributed to study design, simulation models, statistical analyses and manuscript writing.

Chapter 3

Bird diversity and seed dispersal along a human land-use gradient: high seed removal in structurally simple farmland.

Abstract

Only few studies have analysed the relationship between biodiversity and ecosystem function at the landscape scale although relationships and mechanisms known from experimental studies might be different in natural systems. We quantified bird diversity and seed removal from 38 wild cherry trees (*Prunus avium*) along a human land-use gradient from forest to structurally diverse to simple agricultural systems. High human land-use intensity led to low species richness and total abundance of the local bird community around wild cherry trees, as expected from previous studies. Nevertheless, trees in structurally simple agroecosystems were visited as frequently as trees in structurally complex landscapes and in forests. Furthermore, the number of seeds removed per tree did not decline with increasing human land-use intensity. Thus, ecosystem function was robust in spite of locally reduced bird diversity. The reason might be that movement behavior and movement distances of birds changed along the human land-use gradient. It appears that birds moved longer distances to forage in fruiting cherry trees in structurally simple agroecosystems. This suggests that for systems where ecosystem function is mediated by highly mobile organisms, movement behaviour and distances are of considerable importance. Increases in movement distances with increasing human land-use intensity might also be common in other systems in which ecosystem function depends on mobile links.

Keywords: Biodiversity, Ecosystem function, Land-use change, Plant-animal-interactions, Landscpae ecology

Introduction

The relationship between biodiversity and ecosystem function is currently one of the most intensively discussed issues in ecology (Hooper et al. 2005; Kremen and Ostfeld 2005; Balvanera et al. 2006). So far, most research has been conducted using experimental systems with shortlived organisms at rather small spatial scales. However, in a number of recent studies, the focus has turned also towards realistic, non-random changes in biodiversity and to larger spatial scales (Carpenter 1996; Kremen 2005; Steffan-Dewenter et al. 2006; Bracken et al. 2008; Tylianakis et al. 2008b). It is especially important to study the relationship between biodiversity and ecosystem function at the landscape scale since this is the spatial scale at which land-use intensification and associated loss of habitat and biodiversity occur (Harrison and Bruna 1999; Dale et al. 2000; Foley et al. 2005). Landscapes including forests, patches of semi-natural habitats and agroecosystems provide a particularly useful system for the study of the relationship between land-use intensification, biodiversity and ecosystem function (Tscharntke et al. 2005; Kleijn and van Langevelde 2006). The intensity of human land-use can be arranged along a gradient from forest with relatively little human impact to structurally heterogeneous agricultural areas including patches of semi-natural habitats to structurally simple agricultural land with intensive human use. An important question is: how do biodiversity and ecosystem functions change along such a gradient of human land-use (Hooper et al. 2005)? Previous studies demonstrated that land-use intensification has an impact on both biodiversity and ecosystem function. For example, while land-use intensification has no direct effect on parasitism rates in tropical bees and wasps (Tylianakis et al. 2006), it negatively affects pollination rates in a variety of systems (Ricketts 2004; Aguilar et al. 2006; Klein et al. 2007; Ricketts et al. 2008). Tscharntke et al. (2008) found major changes in bird functional groups with land-use intensification, including a large decline in frugivores.

Little is known about the influence of land-use intensification on the interaction between frugivorous birds and fruiting plants (Kremen 2005; Tylianakis et al. 2008a; but see Tscharntke et al. 2008). It is well established that bird diversity decreases along a human disturbance gradient from closed forest to structurally heterogeneous to structurally homogeneous agricultural systems (e.g. MacArthur and MacArthur 1961; Willson 1974; Kati and Sekercioglu 2006). Nevertheless, knowledge about the relationship between human land-use intensity and seed dispersal rates is scarce. Previous studies investigated the effect of forest fragmentation on seed dispersal rates within forests (e.g. Cordeiro and Howe 2003; Farwig et al. 2006; Kirika et al. 2008a, b; Herrera and García 2009) or studied isolated trees within the farmland (e.g. Duncan and Chapman 1999; Slocum and Horvitz 2000; Carrière et al. 2002; Eshiamwata et al. 2006). So far, no study has investigated interactions between birds and fruiting plants along the whole human land-use gradient ranging from forest to structurally complex and simple landscapes.

Seed dispersal is a key process for the spatial and genetic structure of plant populations (Herrera et al. 1994; Bleher and Böhning-Gaese 2001), for the regeneration of disturbed habitats (Tabarelli and Peres 2002), and for vegetation dynamics in general (Schupp and Fuentes 1995; Herrera 2002; Howe and Miriti 2004). In the face of global climate change and increasing habitat fragmentation, seed dispersal is crucial for plant migration (Primack and Miao 1992; Bond 1994). Here, we study the influence of land-use intensification, ranging from relatively undisturbed forest to structurally complex to structurally simple farmland, on the species diversity of local bird communities and on seed removal using the wild cherry (*Prunus avium*) as a model system. We aim to address the following questions: how do the species richness and total abundance of the local bird community change with increasing land-use intensity? How does the species richness and total number of visitors change and the seed removal rate of wild cherry trees change with land-use intensity? We hypothesise that land-use intensification leads to a decline in species richness and abundance of birds in the local bird community, to declines in the species richness and total abundance of visitors and to a decline in seed removal rates. We further test whether foraging behaviour of birds (duration of visits, number of fruits removed per minute and visit) and movement distances after leaving the tree changed along the human land-use gradient.

Materials and methods

Study region

We conducted the study from March to August in 2006 and 2007 in central Germany (Fig. 3.1). The study region covers approximately 3,000 km^2 ranging from Simmern (49°59'N, 7°31'E) in the northwest to Worms (49°38'N, 8°22'E) in the southeast. The region is located in one of the warmest and driest parts of Central Europe. Within the study region, mountain ranges are found in the northwest (Hunsrück, Taunus) and southwest (Donnersberg). These have higher annual precipitation and are covered with mixed deciduous forest. The central area of the study region is intensively used for agriculture (grain, viticulture, rapeseed, vegetables and some pomiculture), and is interspersed with patches of semi-natural habitat such as small woods, hedgerows and isolated trees.

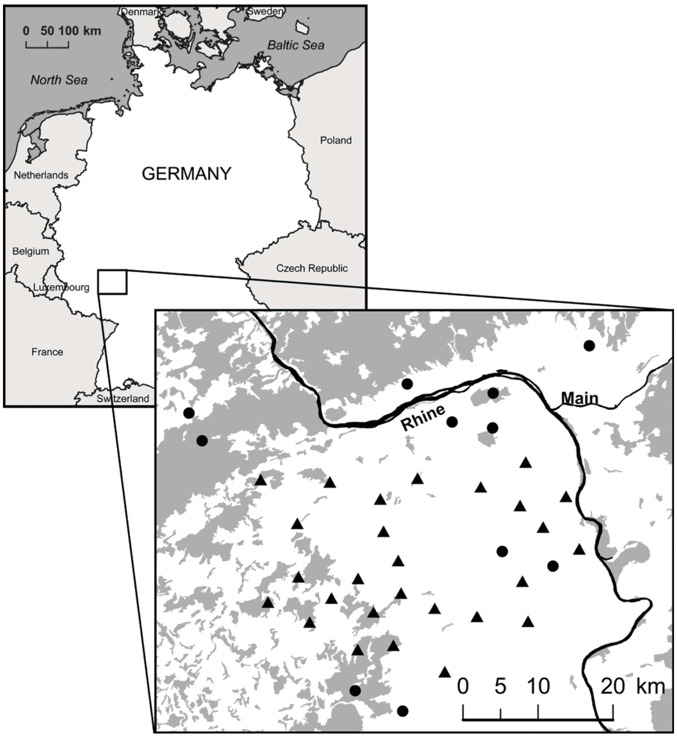

Figure 3.1: Map of the study area in central Germany (*inset* map in background) with the positions of the 38 study trees (trees of 2006 by *filled circles*, trees of 2007 by *filled triangles*). Main rivers are shown in *black*, forests and semi-natural habitats are shown by *grey shaded areas*.

Study species

The wild cherry (*Prunus avium* L.) is highly suitable for our study because it is common and found in a wide range of habitat types with varying intensity of human land-use (Hecker 2001; Höltken 2005). Trees flower in April/May and are insect-pollinated, mostly by bees (Uwate and Lin 1981; Hecker 2001; Conrad 2002). The fruiting period of *P. avium* lasts from June to August (Hecker 2001; Conrad 2002; personal observation). The fruits consist of a fleshy mesocarp which turns from green to red to black during ripening, and a single seed encased in a wooden endocarp. Fruits are roundish with a diameter of 14.7 ± 2.2 mm (mean ± 1 SD, n = 1,674) and weigh 2.0 ± 1.0 g (mean ± 1 SD, n = 1,674). Ripe cherries are consumed and dispersed by a variety of animals (birds, mammals, lizards; Turĉek 1968; Höltken 2005).

Study trees and the structure of habitat and landscape

We selected 11 study trees in 2006 and 27 trees in 2007. We avoided trees that exhibited phenotypic traits typical for sweet cherry cultivars, such as large fruits and low growth forms with widely spread branches. Also, we avoided trees growing in the proximity of sweet cherry orchards. We chose trees under a wide variety of human land-use intensities, ranging from trees in the Taunus and Soonwald, the largest forests in the region, to trees in small, fragmented forests and trees in hedgerows in structurally heterogeneous agricultural areas, to isolated trees in agricultural monocultures. The minimum pairwise distance between the 38 study trees was 4,070 m (Fig. 3.1).

We quantified the habitat and landscape structure in the neighbourhood of the study trees at four different spatial scales. At the smallest spatial scale, we recorded vertical vegetation heterogeneity (verticalVH) within 70 m around each study tree. To do so, we established five circles with a radius of 20 m. One circle was centred at the study tree; the others were centred 50 m to the north, east, south, and west of the tree. We selected this sampling design because it is an efficient design to quantify the local bird community (see next section). Within each circle we estimated plant cover at 0, 1, 2, 4, 8 and 16 m height to the nearest 5 %. We then calculated verticalVH using the Shannon-Wiener diversity index (Bibby et al. 2000) within each circle and averaged verticalVH over the five circles. Trees with high verticalVH were located in structurally complex forests whereas trees with low verticalVH were surrounded by a monolayer of vegetation, e.g. wheat fields.

For the analysis of landscape structure at the three larger spatial scales we used data on the amount of forest and semi-natural habitats at different distances from the trees. We used the CORINE Land Cover 2000 dataset (CLC2000) provided by DLR’s German Remote Sensing Data Center (DLR-DFD 2004) and quantified landscape structure within a radius of 500, 1,000 and 2,000 m around the study trees with a geographical information system (ArcInfo v.9.2 SP4). We then calculated for each radius the proportion of forest and semi-natural areas using land-use types of forest and semi-natural areas (CLC codes starting with 3). Forest and semi-natural habitat types in the study area were: broadleaved forest (14.8 %), mixed forest (6.6 %), coniferous forest (3.4 %), transitional woodland shrub (0.9 %), natural grasslands (0.5 %), moors and heathland (<0.1 %) and sparsely vegetated areas (<0.1 %).

Bird community

To quantify the local bird diversity in the vicinity of each study tree, we estimated species richness and total abundance of birds during the breeding season using point counts. We quantified the bird community in the breeding season, because during this time period detectability is highest and richness and abundance estimates are most precise (Bibby et al. 2000). We counted birds within the five circles with 20 m radius established for recording verticalVH. Within each circle, all birds heard and seen were recorded for a period of 5 min (total 5 × 5 min). By using fixed circles with a relatively small radius (i.e. 20 m), we assume that we recorded a large proportion of the birds present in forest as well as in farmland. We used five circles to increase sample size and to increase the area over which bird species richness and total abundance of the local bird community were estimated. Due to the lower detectability of birds in forest than in farmland, we expected to miss a higher proportion of the birds in the former (Bibby and Buckland 1987). Nevertheless, given the results (see Fig. 3.2), this is a conservative approach.

We started counting 10 min after sunrise and stopped at 11:00 hours Central European Summer Time. In order to count resident as well as migrant species at their time of peak singing activity, we conducted an early bird census (27 March–25 April 2006 and 27 March–10 April 2007) and a second, later census (2–15 May 2006 and 30 April–14 May 2007). All counts were carried out by the same observers (N. Breitbach, I. Laube) and in good weather. For each species, we summed the number of individuals recorded over the five point count locations per census. We then retained for each species the higher of the two values recorded for the two censuses per tree (Marchant 1994; Dunford and Freemark 2004). The five circles were not overlapping but close together. Thus, using our sampling design it is possible that the same bird was counted twice and that abundances tended to be overestimated. Nevertheless, there is no reason to believe that overestimation was biased with respect to the land-use gradient and, given the large differences in total abundance between forest and farmland bird communities (Fig. 3.2), we expect that potential biases caused by this sampling design were of minor importance.

To obtain species richness and total abundances of the local bird community, we summed the number of species and individuals over all species. In this and all following analyses we restricted the analysis to bird species that were observed to eat the fruits and to disperse the seeds of the cherry trees (see next section, and Appendix 2 in the Supplementary Material). We tested species richness and total abundance of seed dispersing birds in the local bird community against human land-use intensity using our measures of habitat and landscape structure at the four spatial scales (i.e. 70, 500, 1,000 and 2,000 m) applying simple linear regressions. Bird abundances were log(x + 1) transformed. For all statistical analyses, we first tested whether the study year and the interactions between year and the respective habitat or landscape variable were significant. Study year and its interaction terms were not significant in any of the analyses. Hence, we pooled the trees from the 2 years and report results only based on the combined data set ($n = 38$). Here and in all following statistical analyses, examination of diagnostic plots indicated that regression model assumptions were not violated. All statistical analyses for this study were conducted in R (R Development Core Team 2005).

Tree visitors and seed removal

We conducted tree observations to quantify species richness and total number of visits of tree visitors and seed removal of wild cherries. We observed trees from 25 June to 20 July 2006 and 13 June to 8 July 2007 at the time when cherries were ripe and the majority of dispersing bird species was still breeding (Bauer et al. 2005). Each tree was observed for 1 day for a time period of 8 h starting at sunrise. Observations were made with binoculars from a hide (tent) placed at a distance of at least 20 m from the tree. All observations were made in good weather. In addition, we recorded cherry colour and ripeness (see below).

For each bird visiting the tree, we recorded species, visit duration, number of dropped, pecked and swallowed cherries, and number of cherries carried away in the beak. If a group of conspecific birds visited the tree and individual behaviour could not be observed simultaneously, we focused on the individual that was best visible. If the behaviour of individuals from different species could not be observed simultaneously, we focused on the rarer species.

We defined all species as seed dispersers of cherries that were observed swallowing cherries or carrying them away in the beak. We decided not to use categorisations from the literature, since not all birds known from the literature as frugivores will act as dispersers in our study region. Furthermore some species that are usually not classified as typical frugivores might, however, occasionally act as seed dispersers of the wild cherry. We determined the number of disperser species and the total number of visits by dispersers for each tree. We calculated the total number of cherries removed per tree per 8 h, summing all cherries that were swallowed or carried away in the beak. To account for missing values, we assessed for each disperser species and tree the mean duration of visits, the mean number of cherries removed per minute spent in the tree and the mean number of cherries removed per visit. If the record of a bird visit for a particular tree was incomplete with regard to duration or seed removal, the missing value was estimated from the mean value for the species and the tree. We used the mean value for the respective tree instead of the global mean over all trees to preserve any possible changes in bird behaviour among trees. For analysis we tested species richness, total number of visits of tree visitors and seed removal against human land-use intensity, i.e. the four measures of habitat and landscape structure. Total number of visitors and number of removed seeds were log(x + 1) transformed.

To investigate whether the foraging behaviour of the birds changed along the human land-use gradient we tested mean duration of tree visits, mean number of fruits removed per minute and mean number of fruits removed per visit against human land-use intensity. The analysis was conducted at the level of the visitor assemblage, i.e. by averaging over all visitors to a tree, regardless of species. We tested mean values over the whole bird assemblage because we were interested in total effects, considering both potential changes in community composition and in foraging behaviour of individual species. Hence, we tested whether mean duration of tree visits, mean number of fruits removed per minute and per visit of the bird assemblage changed with increasing land-use intensity.

For each bird leaving a tree, we estimated the distance the bird flew until it first perched, and the microhabitat in which it perched, thereby noting characteristic landmarks nearby for later verification of estimates through measuring distances by tape or on maps. We also noted whether we lost the bird from sight before it perched. We tested whether mean movement distances increased with increasing land-use intensity. We assume that the distances a bird flies when leaving the tree correlate with the distances the bird flies when approaching the tree and thus are representative for movement distances in the respective landscape. We recorded the microhabitat in which the bird first perched as a simple proxy for the quality of seed dispersal, assuming that birds that perched in forest or semi-natural habitat have a higher probability of transporting the seed to a suitable microhabitat for seedling establishment than birds that perched, for example, in a wheat field.

Spatial effects and confounding variables

We tested the response variables for potential effects of spatial autocorrelation. To this end, we identified the distances for all possible pairwise combinations of the 38 study trees and partitioned these distances into ten distance classes according to Sturge’s rule (Legendre and Legendre 1998). We then examined Morans’s I values for each response variable and distance class. Within the first three distance classes (mean distance of 4.8–13.9 km) none of the response variables showed any significant spatial autocorrelation (Moran's I < 0.180 in all cases).

A potential problem in this non-experimental system is that the study trees differ in fruit availability and fruit traits that might influence the results. Hence, we quantified for each tree on the day on which tree observations were conducted crop size, general fruit availability in the neighbourhood of the tree, fruit size, fruit mass and fruit colour (see Appendix 1 in Supplementary Material). We also recorded temperature and weather conditions. We then included these variables as covariables in multiple regression analyses and tested whether the results changed in comparison to the simple regression analyses. None of the analyses with covariables led to different results, so we report simple regression analyses only.

Sweet cherry cultivars that are mistakenly identified as wild cherries could potentially confound our results. To confirm that we were able to visually distinguish genuine wild cherries from sweet cherry cultivars, we employed genetic analyses for a set of 23 wild cherry trees (11 of these from the analyses presented here), using seven microsatellite markers (see Appendix 1). Genetic analyses demonstrated that our a priori identification of wild cherries was correct in all 23 tested cases.

Results

Bird community

During the bird census in the breeding season, we observed a total of 17 species and 669 individuals that were later identified as seed dispersers of wild cherries during tree observations (see next section). The number of species and individuals in the bird community acting as seed dispersers of wild cherries decreased with declining verticalVH at a tree location (Table 3.1; Fig. 3.2). The number of seed disperser species also decreased with lower amount of forest and semi-natural habitat up to a distance of 2,000 m around the tree (Table 3.1), but verticalVH explained much larger amounts of variation (Table 3.1).

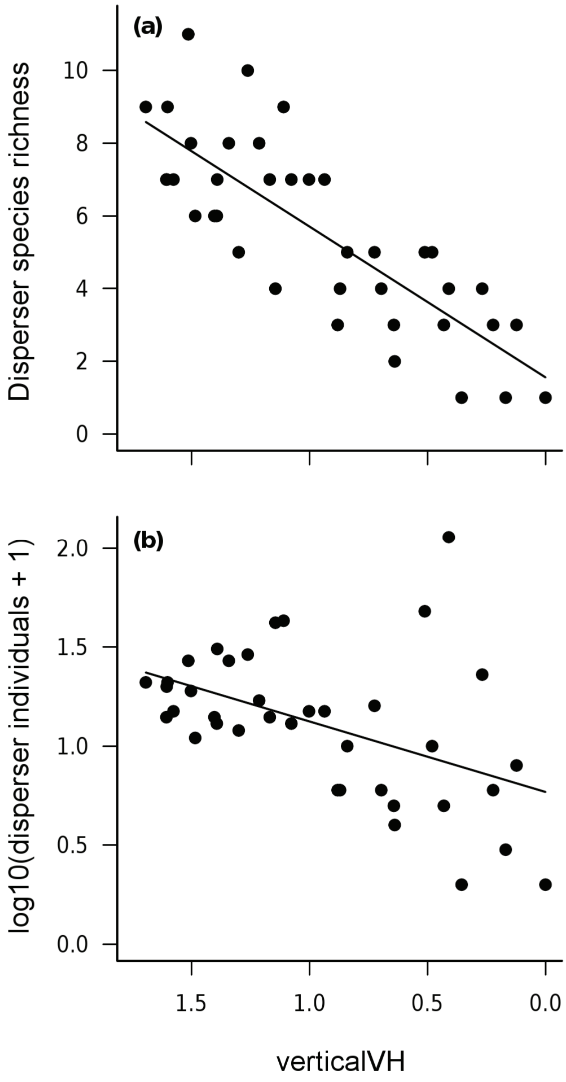

Figure 3.2: Effect of vertical vegetation heterogeneity (*verticalVH*) on **(a)** seed disperser species richness and **(b)** total abundance of seed dispersers in the **local bird community**. As we were interested in the response of the bird community to increasing land-use intensity we plotted the mirror image of the *x*-axis to allow for a more intuitive interpretation of the results.

Table 3.1: Effect of vertical vegetation heterogeneity (*verticalVH*) and the proportion of forest and seminatural habitat (*% seminatural area*) <500 m, <1,000 m, <2,000 m distance from the tree on species richness and abundance of seed dispersers in the local bird community and on species richness and abundance of tree visitors and number of seeds removed.

Response	Landscape structure at different spatial scales (predictor)	*β*	*t*	*P*	R^2
Bird Community					
Seed disperser species richness	**verticalVH (70 m)**	**4.15**	**8.22**	**< 0.0001**	**0.65**
	% seminatural area < 500 m	**0.03**	**2.84**	**0.007**	**0.18**
	% seminatural area < 1,000 m	**0.03**	**2.65**	**0.012**	**0.16**
	% seminatural area < 2,000 m	**0.03**	**2.11**	**0.042**	**0.11**
Seed disperser individuals	**verticalVH (70 m)**	**0.82**	**3.17**	**0.003**	**0.22**
	% seminatural area < 500 m	0.01	1.40	0.170	0.05
	% seminatural area < 1,000 m	0.01	1.35	0.185	0.05
	% seminatural area < 2,000 m	0.01	1.01	0.320	0.03
Tree Visitors					
Seed disperser species richness	verticalVH (70 m)	1.20	1.44	0.153	0.05
	% seminatural area < 500 m	**0.02**	**2.08**	**0.045**	**0.11**
	% seminatural area < 1,000 m	0.03	1.97	0.057	0.10
	% seminatural area < 2,000 m	0.03	1.68	0.102	0.07
Seed disperser individuals	verticalVH (70 m)	0.23	0.51	0.612	< 0.01
	% seminatural area < 500 m	0.01	1.23	0.225	0.04
	% seminatural area < 1,000 m	0.01	1.09	0.282	0.03
	% seminatural area < 2,000 m	0.01	0.81	0.423	0.02
Removed cherries	verticalVH (70 m)	–0.07	–0.12	0.905	< 0.001
	% seminatural area < 500 m	0.01	0.96	0.344	0.02
	% seminatural area < 1,000 m	0.01	0.80	0.432	0.02
	% seminatural area < 2,000 m	0.01	0.45	0.654	0.01

Individuals and removal rates log(x + 1) transformed; n = 38 for all models

Significant relationships are printed in bold

Given are *β*, *t*, *p*, R^2 from simple regression analyses

Tree visitors and seed removal

During 304 h of tree observations we recorded 1,830 visits of 17 species observed dispersing cherries (total number of recorded visits in parentheses): common starling (*Sturnus vulgaris*; 434), common blackbird (*Turdus merula*; 398), Eurasian blackcap (*Sylvia atricapilla*; 274), great tit (*Parus major*; 189), garden warbler (*Sylvia borin*; 96), common chaffinch (*Fringilla coelebs*; 73), great spotted woodpecker (*Dendrocopos major*; 59), song thrush (*Turdus philomelos*; 42), common whitethroat (*Sylvia communis*; 42), common wood pigeon (*Columba palumbus*; 42), Eurasian jay (*Garrulus glandarius*; 36), hawfinch (*Coccothraustes coccothraustes*; 35), mistle thrush (*Turdus viscivorus*; 27), Eurasian golden oriole (*Oriolus oriolus*; 21), Eurasian nuthatch (*Sitta europaea*; 20), carrion crow (*Corvus corone*; 20) and fieldfare (*Turdus pilaris*; 19). Our definition of dispersers is conservative in that it includes all bird species for which we observed dispersal events. Since dispersal sometimes occurred while birds were handling the fruits with the aim of either pecking on the pulp or preying on the seed, our list of dispersers also includes finches and birds with a relatively small gape width.

In contrast to the results for the bird community, species richness and total number of tree visitors did not decrease with declining verticalVH (Fig. 3.3a, b; Table 3.1) nor with the area covered by forest and semi-natural habitat at any of the three larger spatial scales [an exception was the effect of proportion of forest and semi-natural habitat within a 500 m radius on seed disperser species richness, but the amount of explained variance was low ($R^2 = 0.11$); Table 3.1].

The mean number of cherries removed per tree during 8 h of tree observation was 31.4 ± 45.0 (mean ± 1 SD, $n = 38$). Seed removal was not significantly related to verticalVH (Fig. 3.3c; Table 3.1) nor to the amount of forest and semi-natural habitat at any of the three larger spatial scales (Table 3.1). Furthermore, seed removal was not influenced by the species richness or total abundance of seed dispersers in the local bird community (simple regressions: effect of species richness, n.s.; effect of abundance, n.s.). However, seed removal was influenced by the species richness and total number of tree visitors [simple regressions: species richness, $\beta = 0.4$, $t = 5.2$, $P < 0.0001$, $R^2 = 0.41$, $n = 38$; log(number of visitors + 1), $\beta = 1.0$, $t = 9.0$, $P < 0.0001$, $R^2 = 0.68$, $n = 38$].

The mean duration of tree visits or the number of fruits removed per minute or per visit did not change with increasing land-use intensity (Table 3.2). There was a slight, but not significant increase in visit duration with decreasing verticalVH, resulting, however, in a similar number of seeds removed per visit regardless of verticalVH (Table 3.2). Thus, the behaviour of an average tree visitor, regardless of species, did not change along the human land-use gradient.

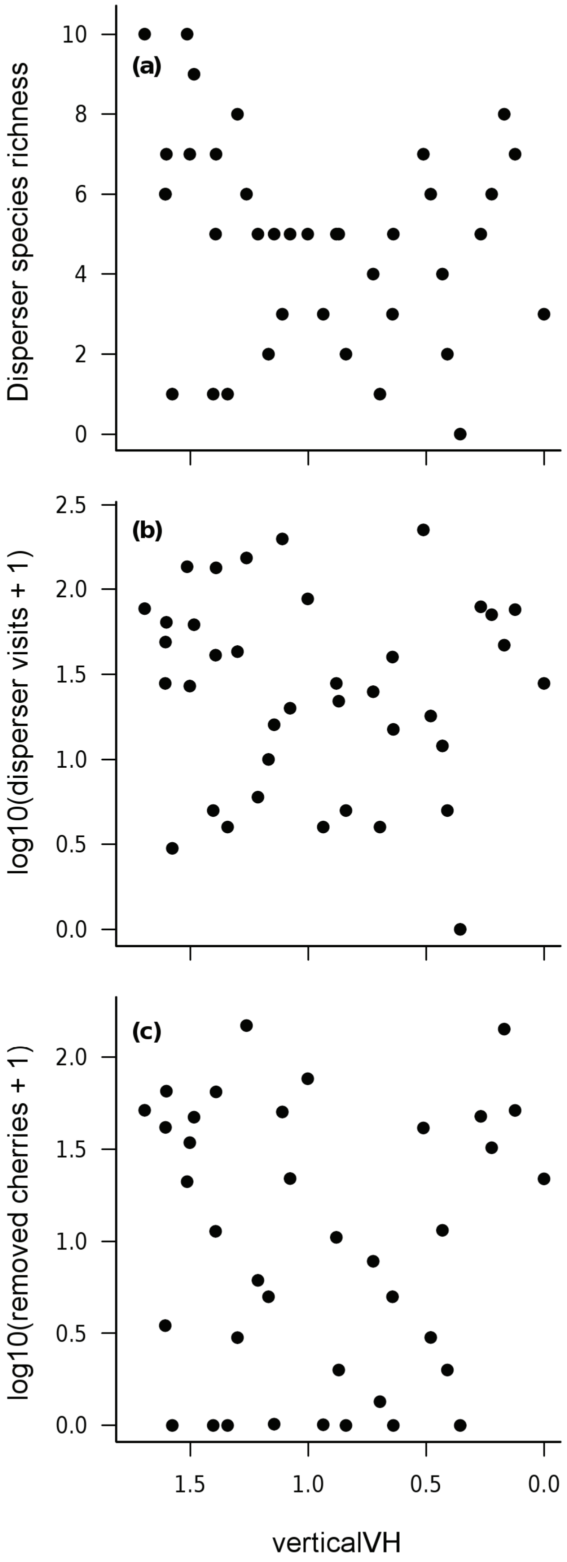

Figure 3.3: Effect of verticalVH on **a** species richness and **b** total number of visits of tree visitors and **c** total number of seeds removed from 38 wild cherry trees. As we were interested in the response of the bird community to increasing land-use intensity we plotted the mirror image of the *x*-axis to allow for a more intuitive interpretation of the results.

For 1,266 out of a total of 1,830 disperser visits, we were able to observe how far birds flew after they left the tree and before they perched again. The mean flight distance was 67 ± 128 m (mean ± 1 SD, range = 0–1,000 m, $n = 1,266$; a flight distance of 0 m was noted when the bird first perched directly under the crown of the focal tree). Birds flew significantly longer distances if verticalVH around the tree was low (Fig. 3.4; Table 3.2). Thus, the higher the human land-use intensity, the longer the birds flew after leaving the tree. There was also a slight trend of increasing leaving distances, if the landscape around the tree was covered by little forest and semi-natural habitat (Table 3.2). The chance of losing a bird from sight after it left the tree was not influenced by differences in verticalVH [simple regression: percentage of birds lost (arcsine square root transformed), $\beta = 0.002$, $t = -0.015$, $P = 0.99$, $R^2 < 0.01$, $n = 37$ (no visitors on one tree)]. In 89 % of the visits ($n = 1,247$), tree visitors flew to forest, groups of trees, into hedges, hedgerows, or shrubs. In 11 % of the visits, a bird's first perch was in agricultural habitats, for example vineyards, orchards, wheat fields or meadows. For comparison, only about 20 % of the area in a 1,000 m radius around the study trees (the maximum flight distance of a bird after leaving the tree) consisted on average of forest and semi-natural habitat.

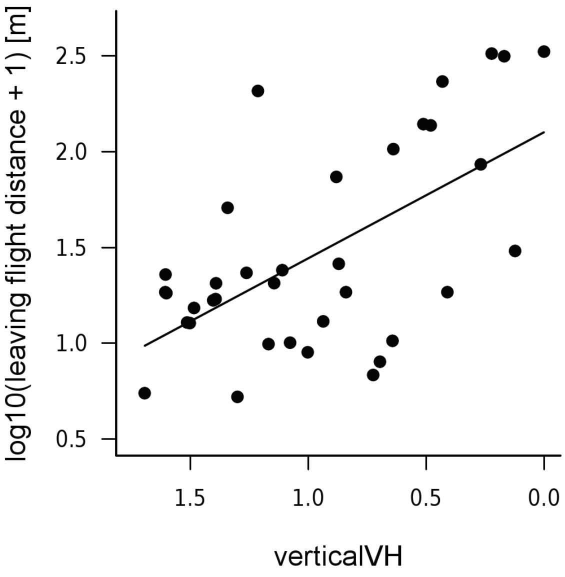

Figure 3.4: Effect of verticalVH on average leaving flight distance from 36 wild cherry trees. As we were interested in the response of the bird community to increasing land-use intensity we plotted the mirror image of the *x*-axis to allow for a more intuitive interpretation of the results.

Table 3.2: Influence of vertical vegetation heterogeneity (*verticalVH*) and the proportion of forest and semi-natural habitat (*% seminatural area*) <500m, <1,000m, <2,000 m distance from the tree on the seed removal behaviour and flight distance to first perch when leaving the tree on the tree visitor assemblage in wild cherry trees.

Response	**Landscape structure at different spatial scales (predictor)**	β	t	P	R^2
Mean visit duration	verticalVH (70 m)	−0.24	−1.92	0.063	0.09
	% seminatural area < 500 m	−0.02	−1.00	0.328	0.03
	% seminatural area < 1,000 m	−0.00	−0.69	0.494	0.01
	% seminatural area < 2,000 m	−0.00	−0.22	0.830	< 0.01
Mean seed removal per minute	verticalVH (70 m)	0.12	1.09	0.285	0.03
	% seminatural area < 500 m	0.00	1.26	0.216	0.04
	% seminatural area < 1,000 m	0.00	1.10	0.281	0.03
	% seminatural area < 2,000 m	0.00	0.72	0.477	0.01
Mean removal per visit	verticalVH (70 m)	−0.06	−0.58	0.569	< 0.01
	% seminatural area < 500 m	0.00	0.40	0.694	< 0.01
	% seminatural area < 1,000 m	0.00	0.28	0.783	< 0.01
	% seminatural area < 2,000 m	0.00	0.08	0.940	< 0.01
Leaving flight distance	**verticalVH (70 m)**	**−1.52**	**−4.42**	**< 0.0001**	**0.36**
	% seminatural area < 500 m	−0.01	−1.97	0.057	0.10
	% seminatural area < 1,000 m	**−0.01**	**−2.08**	**0.045**	**0.11**
	% seminatural area < 2,000 m	−0.01	−1.76	0.088	0.08

All response variables were log(x + 1) transformed. Given are β, t, P, R^2 from simple regression analyses. Significant relationships are printed in bold. n = 36 for the leaving flight distance models; n = 38 for all other models.

Discussion

High human land-use intensity led to a depauperate local bird community around wild cherry trees, but had no influence on tree visitor assemblages and seed removal rates. As expected, the species richness and total abundance of birds in the breeding bird community decreased with increasing human land-use intensity. Nevertheless, in contrast to our expectations, trees in structurally simple agroecosystems were visited as frequently as trees in structurally complex landscapes and in nearby forests. Furthermore, the number of seeds removed per tree did not decline with increasing human land-use intensity.

Both species richness and total abundance of birds in the local community declined in areas where land-use intensity increased and the vegetation became more homogeneous. Such relationships have been widely documented since the classic work of MacArthur and MacArthur (1961; Willson 1974; Billeter et al. 2008). Intensive agricultural use, coupled with the removal of isolated trees, hedgerows and other semi-natural landscape elements inevitably leads to depauperate bird communities (Marzluff and Ewing 2001; Devictor et al. 2008; Herzon et al. 2008). These declines were evident at the level of local bird communities, indicating declines in local population densities and local loss of species.

Local bird communities, as well as tree visitors and leaving flight distance were influenced by habitat structure mostly at the smallest spatial scale (<70 m), and much less so at larger spatial scales (500–2,000 m). The dependence of bird-habitat relationships on spatial scale is well known (Brennan and Schnell 2005; Kristan 2006). Moreover, the resolution of the CORINE data might contribute to the small effects of larger-scale landscape structure on birds in this study. The satellite-derived CORINE data have a limited resolution, i.e. they cannot resolve structures smaller than 100 × 100 m and may thus fail to reflect small landscape elements like bushes, hedgerows and single trees in the agricultural matrix which are important for bird mobility and habitat use.

We did not find a lower species richness of tree visitors, total number of visits or total number of seeds removed for study trees in areas with lower verticalVH (Fig. 3.3). While agricultural monocultures sustained only severely impoverished bird communities, birds found and visited wild cherry trees in even the most heavily degraded agricultural landscapes. One explanation for this result could be that local bird communities were quantified 2–3 months earlier than tree visitors to wild cherry trees. We quantified the local bird community at the beginning of the breeding season because during this period bird detectability is highest and richness and abundance estimates are most precise (Bibby et al. 2000). Nevertheless, at the time when cherries were ripe and we observed the trees, birds advanced in their breeding cycle and might have changed their movement behaviour resulting in a more even distribution of birds between forest and structurally simple farmland. We do not think, however, that changes in movement behaviour caused the patterns we observed for two reasons. First, for the majority of disperser species, the breeding season in Central Europe still includes the time when we counted tree visitors (Bauer et al. 2005), making major changes in territoriality and movement patterns unlikely. The only exceptions are for the European golden oriole and the carrion crow which might start their moult during the tree observation period, but since they contributed only a very small proportion to total seed removal, this would have had hardly any effect on the results. Second, even if movement behaviour changed between the beginning and the end of the breeding season, it is unlikely that the steep decline in species richness and abundance in local bird communities between forest and structurally simple farmland (Fig. 3.2) changed between seasons. Low species richness and abundance in farmland compared to forest is a seasonally robust pattern in Europe (Arnold 1983; Fuller et al. 2001). Thus, it is unlikely that the spatial pattern in bird species richness and total abundance changed between the bird counts and the fruiting season of the wild cherry.

A second explanation is that tree visitors were not only recruited from the local bird community quantified up to 70 m distance from the tree, but also from longer distances. After birds establish territories at the beginning of the breeding season, their home range usually centres on their nest site as they practice central place foraging (Orians and Pearson 1979). However, attractive food sources might entice them to make longer excursions (Herrera 2002). Wild cherries are a very attractive food source for many birds (Snow and Snow 1988; Herrera 2002) and thus can attract foraging birds from neighbouring forests and semi-natural habitats even to isolated trees in the farmland.

Furthermore, it is possible that birds show adaptive movement patterns and compensate for local land-use intensification by flying successively longer distances in structurally poorer landscapes (Fig. 3.4; Sekercioglu et al. 2007). In fact, at one cherry tree at the edge of a wheat field without any forest or semi-natural vegetation within 250 m we observed nine visits by Eurasian golden orioles commuting between the cherry tree and a row of poplars (*Populus* sp.) over 700 m away. Such increasing movement distances are not necessarily expected. Previous studies have shown reduced bird movement distances in clearfelled compared to mature forest and smaller home ranges in fragmented than in continuous forests (Levey et al. 2005; Hinam and St. Clair 2008). In contrast, birds in our study system flew longer distances to reach food resources in structurally poor landscapes and thus functioned as mobile links between patches of semi-natural habitat (Lundberg and Moberg 2003; Sekercioglu 2006).

These results indicate that real-world ecosystems sustain processes and mechanisms that might compensate ecosystem functions at landscape scales that are not evident in mostly small-scale experimental systems. Here, a general decline of bird species richness and total abundance in intensively used agricultural land appears to be accompanied by longer movement distances and the transient aggregation of birds in fruiting cherry trees. Increasing movement distances have been documented not only for birds and seed dispersal. Steffan-Dewenter and Kuhn (2003) found a similar pattern for pollen-collecting bees which had larger foraging distances in simple than in complex landscapes. For systems where ecosystem function is mediated by highly mobile organisms, the influence of foraging movements appears to be of considerable importance (Harris and Reed 2002; Kremen et al. 2007). Despite the practical difficulties in studying species that move over large distances, further research into the foraging movements of birds should be conducted to gain a better understanding of the relationship between biodiversity and ecosystem function in seed dispersal systems (Westcott and Graham 2000; Westcott et al. 2005).

Furthermore, there might be more systems in which mobile links modify the relationship between local biodiversity and ecosystem function, for example pollination systems (Steffan-Dewenter et al. 2002, 2005; Fontaine et al. 2006) or biological control by mobile parasitoids (With et al. 2002; Bianchi et al. 2006). In fact, Dick (2001) reports that introduced African honeybees (*Apis mellifera scutellata*) compensate for the absence of native pollinators of the tropical tree *Dinizia excelsa* in rainforest fragments and open pastures, providing gene flow over an even larger distance than native pollinators (Dick et al. 2003) and thus linking fragmented populations.

By quantifying seed removal rates of trees we recorded only the quantity of seed dispersal, not its quality [e.g. seed dispersal distances, gut treatment, seed deposition site, *sensu* Schupp

(1993)]. Furthermore, seedling and tree establishment is not only shaped by seed deposition patterns, but also by light availability, intra- and interspecific competition, and by predation, herbivory, and parasitism. Thus, at present it is not possible to establish the effects of bird diversity on the recruitment of wild cherry trees in agroecosystems beyond the stage of seed removal.

The analyses of the habitat the birds first perched in after leaving the study trees yield preliminary information on potential seed deposition sites. In almost 90 % of the visits, tree visitors flew to forest or to semi-natural habitats although such habitats comprised only about 20 % of the area within 1,000 m around the study trees. Such patches of semi-natural vegetation appear to be suitable habitats for the successful establishment of wild cherry seedlings (Conrad 2002). In a preliminary study, we measured seed rain of wild cherry seeds at 100 locations in closed forest and 100 locations in patches of semi-natural vegetation within the farmland (hedgerows, small stands of trees) and found that seed rain is similarly high in both habitat types (Wilcoxon test: $W = 4{,}718.5$, $P = 0.47$, $n = 200$).

Birds avoided stopping in unfavourable habitats, such as wheat fields, and instead moved between patches of forest and semi-natural habitat. It might be expected that seeds are also deposited in these patches, potentially leading to directed dispersal of seeds into favourable sites for seedling and tree establishment (Wenny and Levey 1998; Spiegel and Nathan 2007). Thus, birds with their ability to fly appear to link favourable habitats for cherry trees even in the structurally poorest agricultural landscapes. Hence our study suggests that directed dispersal not only occurs to favourable patches within forests (Wenny and Levey 1998) but also between patches of semi-natural vegetation within intensively used agricultural landscapes. Despite this, a cherry tree in an agricultural habitat may achieve high seed removal only if patches of forest and semi-natural habitat occur within a distance from the tree that is within the birds' foraging distance. Examples from other studies show that the visitation rate of seed dispersers may decrease with distance to heterogeneous and structurally diverse habitats (Luck and Daily 2003). We therefore want to guard against extrapolation of our results to larger spatial scales.

Tree visitation and seed removal rates may decline once the landscape is uniformly degraded beyond a certain spatial extent.

Conclusions

To conclude, seed removal of wild cherry trees is surprisingly robust to changes in habitat and landscape structure in spite of the fact that habitat degradation clearly leads to a depauperate local bird community. In our study system, the movement behaviour of birds and possibly adaptive increases in movement distances in structurally poorer landscapes lead to high seed removal rates and potentially directed dispersal of cherry seeds to suitable habitat patches. Such processes might also be common in other systems where ecological function depends on highly mobile organisms, such as pollination systems and interactions between parasites and parasitoids and their hosts.

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Chapter
4

Influence of habitat complexity and landscape configuration on pollination and seed-dispersal interactions of wild cherry trees.

Abstract

Land-use intensification is a major cause for the decline in species diversity in human-modified landscapes. The loss of functionally important species can reduce ecosystem functions like pollination and seed dispersal, but the intricate relationships between land-use intensity, biodiversity and ecosystem functioning are still contentious. Along a gradient from forest to intensively used farmland, we quantified bee species richness, visitation rates of bees and pollination success of wild cherry trees (*Prunus avium*). We analysed the effects of structural habitat diversity at a local scale and of the proportion of suitable habitat around each tree at a landscape scale. We compared these findings with previous studies of seed-dispersing birds and mammals in the same model system and along the same land-use gradient. We found that bee species richness and visitation rates were highest in structurally simple habitats, whereas bird species richness but not their visitation rates were highest in structurally complex habitats. Mammal visitation rates were only influenced at the landscape scale. These results show that different functional groups of animals respond idiosyncratically to gradients in habitat and landscape structure. Despite strong effects on bees and birds, pollination success and bird seed removal did not differ along the land-use gradient at both spatial scales. This suggests that mobile organisms like bees and birds move over long distances in intensively used landscapes and thereby buffer pollination and seed-dispersal interactions. We conclude that measures of species richness and interaction frequencies are not sufficient to understand the ultimate consequences of land-use intensification on ecosystem functioning.

Keywords: Biodiversity, Mutualism, Ecosystem function, Land-use change, Plant-animal interactions

Introduction

Human disturbance causes a continuous loss of natural or semi-natural habitats and ultimately forms intensively utilised landscapes comprising only remnants of the formerly prevailing habitat types (Chapin et al. 2000; Baillie et al. 2004; Tscharntke et al. 2005). These landscape modifications lead to changes in biodiversity (BirdLife 2004; MEA 2005a, 2005b; UNEP 2007), which in turn can result in changes in ecosystem functions (e.g. Chapin et al. 2000; Foley et al. 2005; Larsen et al. 2005; Balvanera et al. 2006). Therefore, the relationship between biodiversity and ecosystem functions has been one of the most intensely discussed issues in ecology in recent years (Hooper et al. 2005; Kremen and Ostfeld 2005; Balvanera et al. 2006). Most of our understanding of these relationships comes from experimental studies with short-lived organisms (Debinski and Holt 2000; Larsen et al. 2005), but we still know very little about real-world ecosystems dominated by long-lived organisms (Carpenter 1996; Kremen 2005; Bracken et al. 2008). Moreover, very few studies have used a single model system to look at multiple taxa and ecosystem functions simultaneously (but see García and Chacoff 2007; Herrera et al. 2011) and have been carried out at a landscape scale (but see Tylianakis et al. 2008b; Farwig et al. 2009).

Pollination and seed dispersal by animals are among the most important mutualistic interactions between plants and animals (Sekercioglu 2006; Bascompte and Jordano 2007; Corlett 2007) and contribute to crucial phases in the life cycle of plants (Jordano et al. 2003; Aguilar et al. 2006; Sekercioglu 2006; Kremen et al. 2007). Most plant species depend on animal pollinators for successful reproduction (Williams 1996; Klein et al. 2006; Kremen et al. 2007; Michener 2007). Because about 35 % of all cultivated plants are animal-pollinated (Klein et al. 2007), pollination is one of the most important ecosystem services for human well-being (Ghazoul 2005). In Europe, almost 85 % of the plant species are primarily pollinated by insects, most of them by bees (Williams 1996). During the last decades, solitary and social wild bees, bumblebees and honeybees have declined in Europe and in the United States, both locally and regionally (Allen-Wardell et al. 1998; Kearns et al. 1998; Steffan-Dewenter et al. 2005). A number of studies have demonstrated that such declines in pollinator diversity can result in reduced pollination success and plant reproduction (Kremen et al. 2002; Klein et al. 2003a, 2003b; Ricketts et al. 2008). Two meta-analyses have reported an overall negative effect of human disturbance, e.g. caused by habitat fragmentation, on bee abundance and species richness (Winfree et al. 2007) as well as on pollination and plant reproduction (Aguilar et al. 2006). Another important process that is crucial for plant regeneration is seed dispersal by animals because seed translocation increases the probability that a seed will find suitable conditions for germination and seedling establishment (Jordano et al. 2003). In the face of global climate change, seed dispersal becomes increasingly important for plant migration (Corlett 2007). However, many animal seed dispersers are susceptible to human disturbance and have decreased in abundance in recent decades (Corlett 2007).

Although human impact may simultaneously alter pollination and seed-dispersal processes in human-modified landscapes (García and Chacoff 2007) very few studies have investigated the effects of land-use intensification on more than one type of interaction. Findings from previous studies were ambiguous and have found both similar (Schulze et al. 2004; Farwig et al. 2009; Herrera et al. 2011) and idiosyncratic responses (García and Chacoff 2007; Tylianakis et al. 2008a) of different functional groups of animals to land-use intensification. Differential responses can be expected if the functional groups have different foraging requirements and/or move at different spatial scales (Ghazoul 2005). For instance, bees may strongly respond to the occurrence of specific microhabitats such as open nesting sites (Westrich 1989a), whereas birds have been shown to respond to the configuration of the landscape at a larger spatial scale (Debinski and Holt 2000; Luck and Daily 2003). One reason for such differences is that the foraging scales and home ranges of insect pollinators are much smaller than those of avian and mammalian seed dispersers (Gathmann and Tscharntke 2002; Breitbach et al. 2010; Grünewald et al. 2010). In comparison to seed-dispersing birds, mammals roam over larger distances (Campos-Arceiz et al. 2008), have longer gut passage times (Grünewald et al. 2010), and are thus able to provide longer dispersal distances than birds (Dennis and Westcott 2007). Therefore, it is important to study the effects of land-use intensification on more than one type of mutualistic interaction involving different functional groups of animals, all having distinct foraging and behavioural traits (Mazerolle and Villard 1999; Brennan and Schnell 2005; García and Chacoff 2007). Hence, studies covering land-use gradients both at a local and at a landscape scale are required to compare the responses between different animal groups and the ecosystem functions they provide.

Landscapes comprising natural and semi-natural habitats as well as farmland of varying land-use intensities provide an excellent opportunity to carry out studies investigating the relationship between human disturbance, biodiversity and ecosystem functioning (Tscharntke et al. 2005). In such landscapes, the consequences of changes in biodiversity can be observed in a natural, non-experimental setting, since different parts of the landscape experience different degrees of human disturbance. Plant species occurring along the entire landscape gradient provide highly valuable model systems for testing the effects of land-use intensity on mutualistic plant-animal interactions. The wild cherry (*Prunus avium* L.) is particularly well suited for such a study because it grows in many different habitat types of different land-use intensity (Hecker 2001). Moreover, wild cherries are pollinated by wild bees, honeybees and bumblebees (Santi 1988) and ripe fruits are eaten and dispersed by birds (Breitbach et al. 2010) and mammals (Grünewald et al. 2010). Thus, wild cherry trees depend on both animal pollinators and seed dispersers and in turn provide important nectar and fruit resources for many animal species.

In this study, we investigate bee species richness, bee visitation rates and pollination success on wild cherry trees along a steep gradient of human land-use intensity both at a small habitat scale and at a large landscape scale in central Germany. We compare the findings of the pollination study with results from two previous studies dealing with bird and mammal seed dispersal of wild cherry trees within the same study area (Breitbach et al. 2010; Grünewald et al. 2010). We expect that insect pollinators respond mostly to changes at a small spatial scale, whereas birds and mammals are influenced by landscape modifications at a large spatial scale. Therefore, the corresponding ecosystem functions may respond differently to human disturbance at the habitat and at the landscape scale. We address the following questions: 1. How do species richness and visitation rates of bees change with habitat complexity at a small spatial scale and with landscape configuration at a large spatial scale? 2. Do different functional groups of animals (bees, birds, mammals) respond differently to the same land-use gradient? 3. What are the ultimate consequences of these changes for pollination success and seed removal of the wild cherry?

Materials and methods

Study region

We conducted our study from April to May 2007 and 2008 in central Germany (Fig. 4.1a). The study region covers approximately 3,000 km^2 ranging from Oberwesel (50°11’N, 7°73’E) in the northwest to Worms (49°38’N, 8°22’E) in the southeast. Average temperature of the coldest and hottest month are 1.1 °C (January) and 19.0 °C (July), respectively. Annual rainfall is ca. 500 mm with higher rainfall between May and August. Mountain ranges covered with deciduous forest are found in the northwest (Hunsrück, Taunus) and southwest (Donnersberg). The central area of the study region is intensively used for agriculture (grain, wine, rapeseed, vegetables and some pomiculture), interspersed with patches of semi-natural habitat such as transitional woodland-shrub, hedgerows, pastures and natural grasslands.

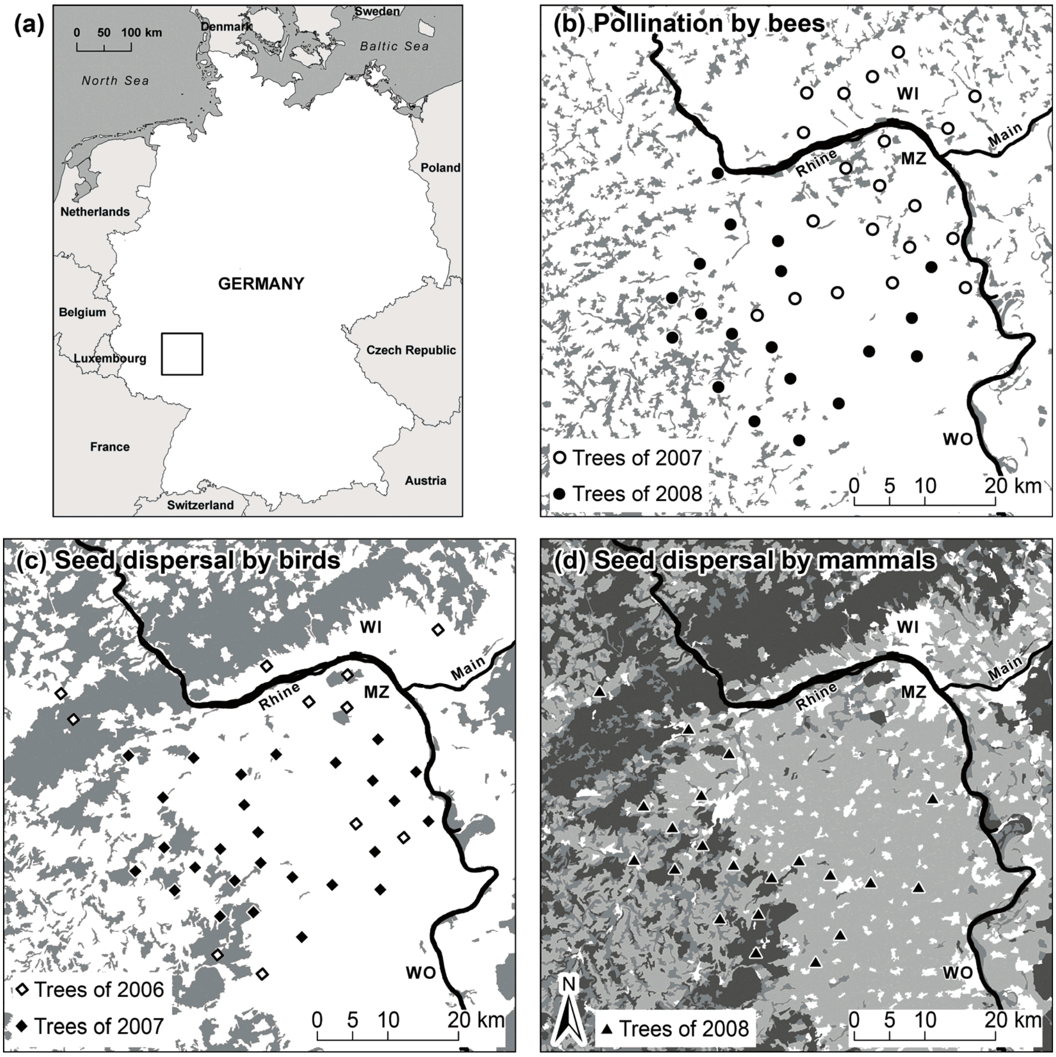

Figure 4.1: (a) Location of the study area in central Germany (indicated by *square*; **(b)** positions of 32 study trees used for the analysis of pollination by bees (2007, 2008); (**c**) 38 study trees used for analysis of seed removal by birds (2006, 2007); and **(d)** 21 study trees used for the analysis of seed removal by mammals (2008). Courses of main rivers are shown in black (i. e. Rhine and Main); cities abbreviations are WI (Wiesbaden), MZ (Mainz) and WO (Worms). Suitable habitat for bees, birds and mammals is indicated on each map (*grey shaded areas*).

Model system

The wild cherry, *Prunus avium* L. (Rosaceae) is a deciduous, broadleaf tree that is native to Eurasia and grows up to 15–20 m (rarely 30 m) high. The species is early-successional and occurs in a wide range of habitats including deciduous mixed forest, forest edges, woodland, hedgerows and fallows. The wild cherry produces white flowers on long pedicels which are borne in umbels of 2–6 flowers; neighbouring umbels often form larger aggregates. Flowers are hermaphroditic and self-incompatible (Schueler et al. 2006). Trees flower early in April/May and are insect-pollinated, mostly by bees (Hecker 2001); the flowering period of an individual tree lasts for about one week. The fruit is a drupe with a single seed. The fleshy mesocarp turns from green over red to glossy black during ripening; the fruiting period of *P. avium* lasts from June to August (Hecker 2001; Breitbach et al. 2010). Ripe cherries are consumed and dispersed by a variety of animals (birds, mammals, lizards) (Turĉek 1968; Breitbach et al. 2010; Grünewald et al. 2010).

Study trees and structure of habitat and landscape

We selected 32 wild cherry trees in 2007 and 2008 to investigate bee species richness, visitation rates and pollination success (Fig. 4.1a). We chose trees with similar crown volume and avoided trees that exhibited phenotypic traits typical for sweet cherry cultivars, such as large fruits and low growth forms. We also avoided trees growing in the proximity of sweet cherry orchards. We chose trees under different human land-use intensities, ranging from trees in larger forests, over trees in small, fragmented forests and trees in hedgerows in structurally heterogeneous agricultural areas, to isolated trees in agricultural monocultures. The pairwise distance between study trees was never smaller than 4,200 m (Fig. 4.1).

We quantified the habitat and landscape structure in the neighbourhood of the study trees at different spatial scales using two different methods. At the small spatial scale, we recorded vertical vegetation heterogeneity (in the following verticalVH) within 70 m around each study tree (5 circles with 20 m radius to sample the whole 70 m radius) and calculated the Shannon-Wiener diversity index as a measure of local structural complexity of the habitat (for more details see Breitbach et al. 2010). For the analysis of landscape structure at the larger spatial scale, we used data on the amount of forest and semi-natural habitats at different distances from the trees (1,000 and 2,000 m radius). We used the CORINE Land Cover 2006 dataset (hereafter called CLC2006) provided by DLR’s German Remote Sensing Data Center (DLR-DFD 2009) and quantified landscape structure within 1,000 and 2,000 m radii around all study trees with a geographical information system (ArcInfo v.9.3 SP1) (for more details see

Breitbach et al. 2010). From the set of predefined CLC2006 categories, we defined appropriate sets of suitable habitats for bees, accounting for the specific habitat requirements of bees. These suitable habitat types include: structurally simple and open habitats such as grassland, meadows and extensively used farmland (see Table A3.1, Appendix 3). We calculated the proportion of suitable habitat in radii of 1,000 and 2,000 m. As the results from the two radii were closely correlated (Pearson correlation: $r = 0.85$; $P < 0.001$), we only report results for two spatial scales: the verticalVH at the small spatial scale and the proportion of suitable habitat within the 2,000 m radius around each tree at the large spatial scale.

Local bee community

To quantify the *local bee community* (i.e. honeybees, wild bees and bumblebees) in the vicinity of each study tree, we quantified the species richness of bees during the flowering period of the wild cherry (05.04.–19.04.2007 and 06.04.–04.05.2008) using pan traps (Potts et al. 2005; Westphal et al. 2008). To enhance the attractiveness, bowls were coated with UV light reflecting fluorescent spray-paint (SPRAY-COLOR GmbH, Merzenich, Germany). We deliberately used white instead of yellow pan traps (contrary to recommendation by Potts et al. 2005) because our aim was to quantify the pollinators that forage on white cherry flowers.

We used a total of six pan traps for each study tree. Four traps were placed in 20 m distance from the tree in each compass direction. A fifth trap was placed directly under the tree crown next to the trunk. A sixth trap was lifted into the tree crown using a thin nylon thread. Traps were open for a 48 h period. Afterwards, the content of each bowl was passed through a sieve; the retained insects were later identified to species level using standard references (see Appendix 5) and reference collections at the University of Bayreuth (I. Steffan-Dewenter). We calculated the species richness of bees per tree by calculating the mean number of species per trap for each tree. Pollinators that did not belong to any of the three bee guilds (i.e. a few beetles and fruit flies) were excluded from further analyses.

Visitation rates of pollinators

To quantify the *visitation rate of tree-visiting pollinators*, we conducted tree observations from 05.04.–19.04.2007 and from 06.04.–04.05.2008 at a time when at least two thirds of all flowers on a cherry tree were fully opened. All trees were visited twice on different days. To avoid potential influences caused by pan traps, we performed the observations at times when no trapping took place. We conducted observations between 10:00 and 17:00 hours at times when bees are most active. On each tree, three branches with aggregates of 50 flowers were randomly chosen and then observed with spotting scopes (Zeiss Diascope 65 T* FL and 85 T* FL) for 10 minutes. All observations were made in good weather on warm days. For each ten minute observation interval, we recorded the number of bees that visited flowers (honeybees, wild bees and bumblebees). For each tree, we recorded visitation rates for 60 minutes (2 days × 30 minutes) on six different branches (2 days × 3 branches). Mean visitation rate was calculated as the number of bee visitors per observation interval and thus it measures how many bee individuals visit a flower aggregate with 50 flowers during ten minutes. A potential problem in this non-experimental system is that the study trees differed in the number of flowers and that the number of other flowers in the tree neighbourhood could also influence the results. Hence, we estimated for each tree the number of open flowers and the general flower availability in the neighbourhood of each tree (50 m radius).

Pollination success

To determine *pollination success* of wild cherry trees, we selected three branches on each of 32 study trees (12 in 2007 and 20 in 2010) during the flowering time of the wild cherry, and marked 100 flowers on each branch. For reaching branches of high farmland trees (e.g. within hedgerows) and of forest trees (height ≥ 20 m), we used mobile access platforms (WUMAG LT 220 K D and LT 250 K D; provided by mateco AG, Frankfurt). We returned to the marked branches after about four weeks and recorded seed set as the number of swollen ovaries for each of the 100 flower-aggregates. We recorded the state of fruit formation as a) no fruit, b) dwarfed fruit (i.e. aborted at an early stage), c) depredated fruit or d) healthy green fruit. Since we were interested in pollination success (not seed production), we assumed that categories b to d indicate fertilisation and thus successful pollination. Hence, pollination success was the mean proportion of fruits in these three categories over all three branches per tree.

Species richness and visitation rates of seed dispersers and seed removal

We compared the results of the bee and pollination studies with two previous studies of seed-dispersing birds (Breitbach et al. 2010) and mammals (Grünewald et al. 2010). We employed the same measures for local habitat complexity and habitat suitability at the landscape scale (2,000 m radius) for each cherry tree included in these studies. In difference to the previously published studies (Breitbach et al. 2010; Grünewald et al. 2010) and corresponding to the pollination analyses, we used the CLC2006 data to determine habitat suitability at the landscape scale. According to the previous studies, we defined forest and structurally complex semi-natural habitats as suitable habitat for birds (see Table A3.1, Appendix 3). In the study area, extensively used farmland is the main foraging habitat of mammals (Grünewald et al. 2010) and was classified as suitable habitat for mammals (see Table A3.1, Appendix 3). The landscape gradient was similar for all three functional groups ranging from cherry trees growing in landscapes with high proportions of suitable habitat to trees growing in unsuitable, intensively used landscapes (Fig. 4.1).

Bird species richness was recorded in 5-minute point counts at 38 wild cherry trees from March to May in 2006 and 2007; *visitation rates* of avian tree visitors were recorded during 8-hour observations in June and July 2006 and 2007 on the same wild cherry trees. To determine visitation rates, we counted the number of individuals of all bird species that had been observed to swallow cherries or to carry them away in the beak. To determine *seed removal* by avian seed dispersers, we recorded the number of fruits that were swallowed or carried away (for details see Breitbach et al. 2010). In 2008, *visitation rates* of mammalian tree visitors were recorded under 21 study trees for three consecutive nights using camera traps. *Visitation rate of mammals* was defined as the total number of photographs with mammalian visitors (for details see Grünewald et al. 2010).

Statistical analyses

All statistical analyses were conducted in R 2.10.1 (R Development Core Team 2009). Bee visitation rates were log10(x + 1) transformed, while proportions (percentage of suitable habitat and pollination success) were arcsin(√x) transformed (Quinn and Keough 2002). In all linear models, the evaluation of diagnostic plots indicated that model assumptions were not violated. Prior to other analyses of bee data, we tested whether the study year and the interaction between year and the respective habitat or landscape variable were significant; this was not the case in any of these analyses. Hence, we pooled trees from consecutive years and report results from the combined data set (n = 32 trees; seed set n = 32 trees). In simple regression models, we tested the effects of habitat heterogeneity on a small spatial scale (i.e. verticalVH in 70 m radius) and landscape suitability on a large spatial scale (i.e. proportion of suitable habitat in 2,000 m radius) on 1. species richness of bees, 2. visitation rates of bees, and 3. pollination success. Predictor variables for the habitat and landscape scale were not significantly correlated (Pearson correlation: species richness: r = 0.32, P = 0.075). To account for differences in flower availability on the tree and in the surrounding of the tree, we additionally carried out multiple regression analyses including the two control variables and the habitat or the landscape variable. However, none of these multiple analyses resulted in qualitatively different effects of the habitat and landscape variables. In addition, to compare the strength of the effects of the habitat and the landscape variable, we calculated four linear models for each response variable (i.e. bee species richness, visitation rates and pollination success). The goodness of the four models (i.e. the three possible combinations of the two predictor variables plus a null model including only the intercept) was compared according to the corrected Akaike's information criterion (AICc). Finally, we calculated the Akaike weight for each model and summed the Akaike weights for each predictor over all models including the respective variable (Burnham and Anderson 2002). The Akaike weight gives the likelihood that a model is the best available model, and thus the summed Akaike weight measures the relative importance of each variable in contributing to the best model; higher weights indicate more important variables (Burnham and Anderson 2002).

We tested the residuals of all simple regression models for potential effects of spatial autocorrelation using the spdep package in R (Bivand et al. 2010). First, we identified the four nearest neighbours of each study tree location for bees ($n = 32$) and then calculated the distance between all resulting tree pairs to obtain a distance matrix. We then converted the distance matrix into a spatial weights matrix using rows standardisation (i.e. weights for each areal entity are standardised to sum to unity; see Bivand et al. 2010). Finally we examined *Morans's I* values and their significance from tests with the residuals of each model and the corresponding spatial weights matrix. To correct for spatial autocorrelation, we performed spatial autoregressive error model estimations (SARs) for the few models where this was necessary. SAR corrections did not change the results qualitatively (see Table A4.1, Appendix 4); in the results section we only report results from models without SAR corrections.

To compare the results from the pollination study with the results from the two previous seed-dispersal studies, we calculated simple regression analyses for the effects of local habitat structure and landscape configuration [arcsin(√x) transformed] on bird species richness, bird and mammal visitation rates [log10(x + 1) transformed] and bird seed removal [log10(x + 1) transformed]. The results from the landscape-level analyses are slightly different from the previous studies (see Breitbach et al. 2010, Grünewald et al. 2010) because we consistently used the recently released CLC2006 data. Fruit availability in the surroundings of the cherry trees did not affect any of the response variables (see Breitbach et al. 2010, Grünewald et al. 2010). Spatial autocorrelation did not affect the results of the simple regression models (see Table A4.1, Appendix 4).

Results

Local bee community, flower visitors and pollination success

During 1,536 hours of trapping on 32 study trees, we recorded a total number of 1,304 individuals of 82 bee species: 15 honeybees (*Apis mellifera*), 1,269 individuals of wild bees (74 species) and 20 individuals of bumblebees (7 species; genera: *Bombus* and *Psithyrus*) (see

Table 5.1, Appendix 5). Species richness of bees (i.e. honeybees, wild bees and bumblebees grouped together) in the local community decreased with verticalVH at the small spatial scale ($r = –0.43$, $P = 0.013$, $n = 32$; Fig. 4.2a), i.e. species richness was lower in structurally complex habitats. In contrast, there was no relationship between species richness and the proportion of suitable habitat in a radius of 2,000 m around a study tree at the large spatial scale ($r = –0.03$, $P = 0.882$, $n = 32$; Fig. 4.2b). In multiple model comparisons, the best model only included verticalVH (Table 4.1, Appendix 4); the Akaike weight for verticalVH was more than three times larger than the proportion of suitable habitat (Table 4.1).

Table 4.1: Effects of vertical vegetation heterogeneity (*verticalVH*) at the small spatial scale and of the proportion of suitable habitat at 2,000 m radius on species richness, visitation rates of bees and mean seed set of cherry trees. Akaike weights (AICc) were calculated for four linear models for each response variable and were summed for each predictor over all models including the respective variable. These weights (range: 0–1) measure the relative importance of each variable in contributing to the best model; higher weights indicate more important variables.

Predictor	**Akaike weight**
a) Species richness	
verticalVH < 70 m (small scale)	0.897
% suitable habitat < 2,000 m (large scale)	0.258
b) Visitation rate	
verticalVH < 70 m (small scale)	0.616
% suitable habitat < 2,000 m (large scale)	0.596
c) Pollination success	
verticalVH < 70 m (small scale)	0.231
% suitable habitat < 2,000 m (large scale)	0.277

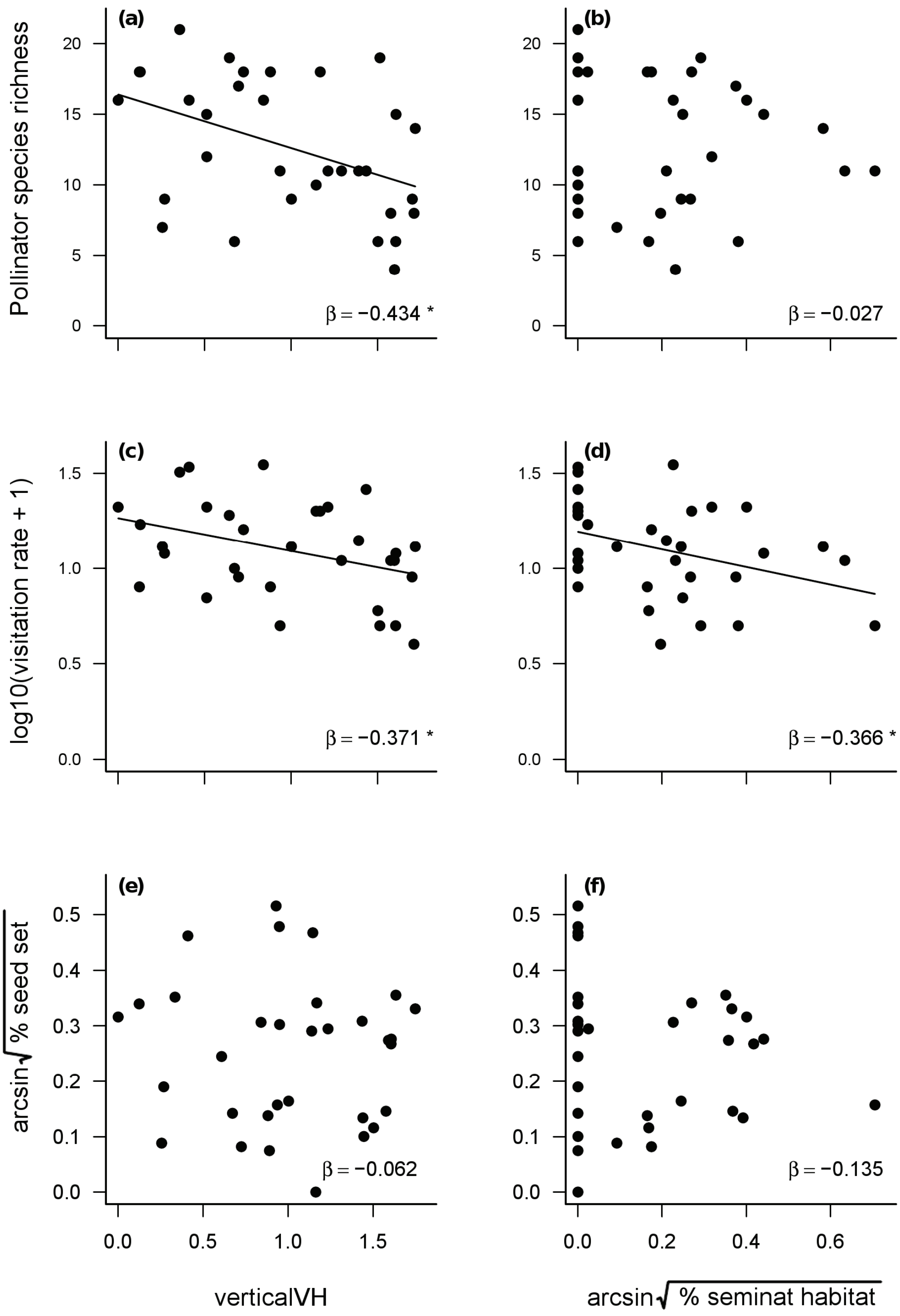

Figure 4.2: Relationships between vertical vegetation heterogeneity (*verticalVH*) and **(a)** pollinator species richness (i.e. honeybees, wildbees and bumblebees), **(c)** visitation rates of bees and **(e)** mean seed set (i.e. percentage of pollinated flowers) in the local species community. Effect of the proportion of suitable habitat at 2,000 m radius around 32 wild cherry trees (taken from the CORINE CLC2006 data set) on **(b)** pollinator species richness on **(d)** visitation rate of bees and **(f)** mean seed set. The standardised regression coefficient (*β*) is given for each relationship of significance level from simple regression analyses: *** = $P \leq 0.001$; ** = $P \leq 0.01$; * = $P \leq 0.05$

During 32 h of tree observations, we recorded a total number of 436 bees (177 honeybees, 214 wild bees and 45 bumblebees) that visited the wild cherry flowers. Bee visitation rates decreased with verticalVH at the small scale (*r* = –0.37, *P* = 0.037, *n* = 32; Fig. 4.2c) and with the proportion of suitable habitat at the large scale (*r* = –0.46, *P* = 0.039, *n* = 32; Fig. 4.2d), i.e. visitation rates were lower in structurally complex habitats and in landscapes with a high proportion of suitable habitat. The goodness of both simple and the multiple regression models were very similar (Table A6.1, Appendix 6); both predictors had similarly large Akaike weights (Table 4.1).

Pollination success was not related to verticalVH (*r* = –0.06, *P* = 0.74, *n* = 32; Fig. 4.2e) or the proportion of suitable habitat (*r* = –0.14, *P* = 0.461, *n* = 32; Fig. 4.2f). The best linear model only included the intercept, and the Akaike weights for both predictors were small (Table A6.1, Appendix 6; Table 4.1).

Comparison between the different functional animal groups

Species richness of avian seed dispersers in the local bird community strongly increased with verticalVH at the small scale (*r* = 0.81, *P* < 0.001, *n* = 38; Fig. 4.3a) and with the proportion of habitat suitable for birds at the large scale (*r* = 0.38, *P* = 0.019, *n* = 38; Fig. 4.3a). In comparison, species richness of bees decreased with verticalVH at the small spatial scale (Fig. 4.3a) and was not related to the percentage of suitable habitat at the large spatial scale (Fig. 4.3a).

Bird visitation rates did not increase with verticalVH (*r* = 0.08, *p* = 0.612, *n* = 38; Fig. 4.3b) and with the proportions of suitable habitat at the large spatial scale (*r* = 0.15, *P* = 0.373, *n* = 38; Fig. 4.3b). The visitation rates of the mammalian dispersers were not related to verticalVH at the small scale (*r* = 0.07, *P* = 0.767, *n* = 21; Fig. 4.3b), but significantly increased with the proportion of habitat suitable for mammals at the large scale (*r* = 0.50, *P* = 0.020, *n* = 21; Fig. 4.3b). In comparison, bee visitation rates decreased with verticalVH at the small scale (*r* = –0.37, *P* = 0.037, *n* = 32; Fig. 4.3b) and also decreased with the proportion of suitable habitat at the large scale (*r* = –0.46, *P* = 0.039, *n* = 32; Fig. 4.3b).

There were no relationships between seed removal by birds and verticalVH (*r* < 0.01, *P* = 0.966, *n* = 38; Fig. 4.3c, *hollow diamond*) and between seed removal and the proportion of suitable habitat at the large spatial scale (*r* = 0.15, *P* = 0.384, *n* = 38; Fig. 4.3c). This pattern is congruent with the weak relationships between pollination success and verticalVH (*r* = –0.06, *P* = 0.74, *n* = 32; Fig. 4.3c), and the proportion of suitable habitat (*r* = –0.14, *P* = 0.461, *n* = 32; Fig. 4.3c).

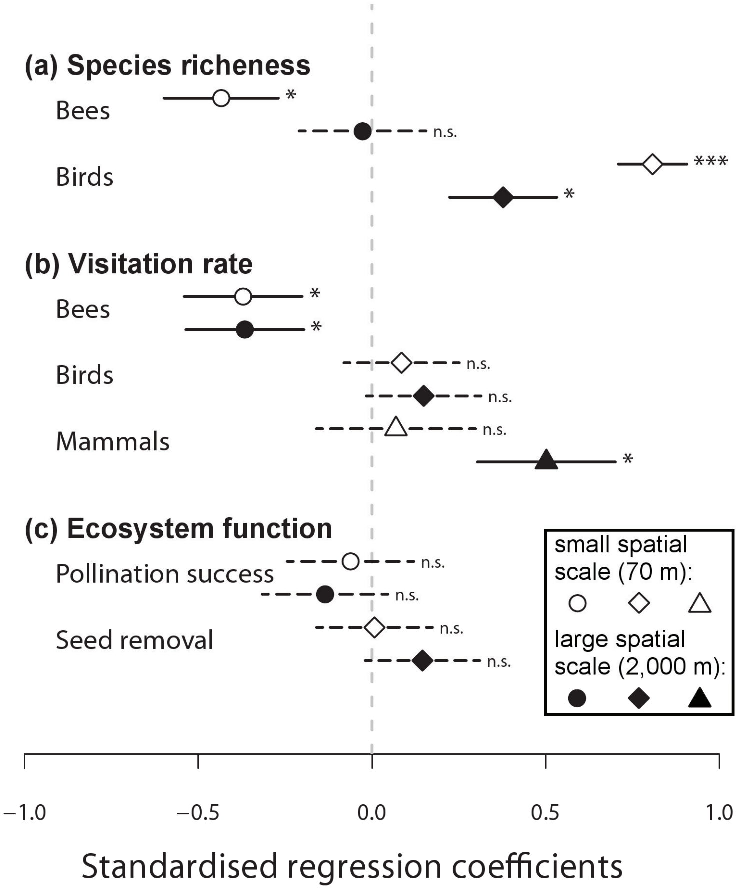

Figure 4.3: Relationships between land-use intensity at two spatial scales and **(a)** species richness of bees and birds, **(b)** visitation rates of bees, birds, and mammals at cherry trees and **(c)** the pollination and seed removal. Shown are the standardised regression coefficients and their standard errors (± 1 SE). Significance of standardised regression coefficients are indicated: *** = $P \leq 0.001$; ** = $P \leq 0.01$; * = $P \leq 0.05$; *n.s.* = non-significant relationships are shown with *dashed* lines.

Discussion

Local bee community

Species richness of bees increased in open habitats but was not related to habitat changes at the landscape level. Open habitats with little vertical structure offer bees many opportunities for suitable nesting sites. Almost all species of wild bees and bumblebees in the study area are ground-nesting (Westrich 1989a) and therefore depend on sunlit open microhabitats for nesting (Westrich 1989b; Schmid-Egger et al. 1995; Westrich 1996). Apart from semi-natural habitats such as meadows or pastures, patches of the agricultural matrix also offer foraging and nesting sites for bees. Bees may build their endogean nest cavities into unpaved roads, fallow land and field boundaries with ditches and small strips of grassland. Indeed, species of the genus *Andrena* were frequently observed nesting in patches of sandy roads in between fields (N. Breitbach and S. Tillmann, personal observation). Hence, our measurement of local habitat complexity (verticalVH) potentially integrates information about both suitable foraging and nesting sites.

In contrast to the strong effect at the local scale, bee species richness did not respond to the landscape configuration at a larger spatial scale. This is supported by a previous study where wild bees responded to the proportion of suitable habitat only at rather small spatial scales (Steffan-Dewenter et al. 2002). Moreover, Gathmann and Tscharntke (2002) examined foraging distances between nesting sites and suitable food plants for 16 wild bee species and found maximum flight distances ranging from 150 to 600 m. Another reason for the lack of a relationship at the large spatial scale could be the coarse spatial resolution of the CLC2006 data set (resolution ca. 1 ha). To account for this uncertainty, we additionally recorded the proportion of suitable habitat within radii of 250 and 500 m around each study tree in the field (data from site inspections not shown). With this approach, we were able to detect suitable habitat patches for bees with a higher accuracy and spatial resolution. Nevertheless, bee species richness did not respond to the proportion of suitable habitats at larger spatial scales (simple linear regressions: 250 m radius: $r = 0.02$, $P = 0.902$; 500 m radius: $r = 0.06$, $P = 0.735$; $n = 32$ in both cases). These results suggest that bees respond more strongly to specific habitat features at a local scale than to the landscape configuration at the large spatial scale.

Visitation rate(s) of pollinators

Visitation rates of bees decreased with habitat complexity at the small spatial scale and also with the proportion of suitable habitat at the large spatial scale. Visitation rates of bees only slightly increased with bee species richness (Pearson correlation: $r = 0.34$, $P = 0.055$, $n = 32$). The weak relationship between species richness and visitation rates might suggest that flower resources were homogeneously distributed over the landscape because the diversity-ecosystem function relationship increases with resource heterogeneity (Tylianakis et al. 2008b). In our system, flower availability differed very strongly among cherry trees (range of estimated flowers per tree: ~2,000–65,000), but these differences did not affect bee species richness (Pearson correlation: $r = 0.21$, $P = 0.253$, $n = 32$). This shows that heterogeneous resource availabilities did not affect bee species richness but probably resulted in changes in bee behaviour.

At the large spatial scale, bee visitation rates decreased with the proportion of suitable habitat. A low proportion of suitable habitat appeared to result in a concentration of bees on the few nectar and pollen resources available; this is consistent with a previous study in Dutch agricultural landscapes (Kleijn and van Langevelde 2006). In our study area, food resources are rare in April when rapeseed or other nectar-rich crops are scarce; wild cherry trees are therefore a primary nectar source early in the year. A patchy distribution of wild cherry trees, in particular in intensively used landscapes, may result in long flight distances of bees to isolated trees and in a strong aggregation of bees at these trees. In a previous study, foraging flights of honeybees were longer in structurally simple than in structurally complex landscapes (Steffan-Dewenter and Kuhn 2003). Bumblebees also undertake longer flights when resources within their usual foraging range are limited (Westphal et al. 2006). Consistent with these studies, our findings support the idea that bee pollinators can compensate a depauperate landscape structure by increasing their foraging distances.

Pollination success

Despite higher visitation rates of bees on trees in structurally simple habitats and in less suitable landscapes, fruit formation was not affected by the gradients in habitat complexity and landscape configuration. Pollination success of wild cherries was not related to the visitation rates of bees (Pearson correlation: $r = -0.06$; $P = 0.757$, $n = 32$), suggesting that fruit formation was not pollinator-limited. This is consistent with the rather high frequencies of bee visits (> 3 visits during 10 minute intervals), even on trees with the lowest visitation rates.

In addition to the number of visitors (i.e. pollen quantity), the origin of deposited pollen (i.e. pollen quality) can strongly affect reproduction (Aizen and Harder 2007). Pollen origin might be particularly important in our system since wild cherry trees are self-incompatible (Schueler et al. 2006). Previous studies of self-incompatible plants have reported that high rates of geitonogamy lead to reduced fruit and seed set (Finer and Morgan 2003; Hirayama et al. 2005; Schleuning et al. 2011). Hence, the decoupling of pollinator visitation rates and fruit formation in our system could be related to differences in bee foraging behaviour and thus in the quality of deposited pollen in different landscapes. In intensively used landscapes, the scarcity of other suitable nectar and pollen resources might force bees to stay longer at a single tree. This is in line with the optimal foraging theory (Charnov 1976) that predicts longer visits on isolated resources in landscapes with patchily distributed resources (e.g. Pyke 1979; Goulson 2000). Consequently, in structurally simple landscapes, bees visit more flowers on a single tree and increase the proportion of self-pollen and thus the degree of geitonogamy (Ghazoul 2005). In addition to the effects of geitonogamy, fruit formation might also be affected by the performance of the mother plant which is influenced by abiotic factors, such as nutrient availability or microclimatic conditions (Ghazoul 2005; Knight et al. 2005; Wesselingh 2007). In this observational study, it was impossible to control for differences in these abiotic factors along our gradient of land-use intensity.

Comparison between the different functional animal groups

Gradients in habitat and landscape structure affected bee and bird communities differently. In contrast to bees, *species richness* of birds in the *local community* increased with habitat complexity and with the proportion of suitable habitat at the landscape scale. Bird species richness was particularly high in forest because most frugivorous birds are forest or woodland species. Previous studies also found that open landscapes with only a few isolated trees or hedgerows hold depauperate bird communities (Marzluff and Ewing 2001; Devictor et al. 2008). In contrast to birds, bees require open habitat types for feeding and nesting and therefore responded very differently to the land-use gradient at the small and the large spatial scale.

Along the gradients of habitat structure and landscape configuration, *visitation rates* of bees, mammals and birds decreased, increased or remained constant, depending on the taxonomic group considered. Despite a strong decline in bird species richness in structurally simple habitats, trees growing in such habitats were visited as frequently by birds as trees in structurally complex landscapes; visitation rates on wild cherry trees were not related to bird species richness (Pearson correlation: $r = 0.27$, $P = 0.102$, $n = 38$). Similar to the behavioural changes of bees, the long flight distances of birds in depauperate agricultural landscapes (Luck and Daily 2003; Lenz et al. 2011) buffered the potential decrease in avian seed removal rates in response to land-use intensification (Breitbach et al. 2010). Longer flight distances of birds in structurally simple habitats even suggest that probabilities of long-distance seed dispersal are higher in such habitats (Breitbach et al. 2010; Lenz et al. 2011). Our findings provide important evidence for the concept that mobile organisms, such as birds and bees, can act as mobile links between patchily distributed habitats (Lundberg and Moberg 2003; Sekercioglu 2006) and the former more theoretical concept of mobile link compensation has now empirically proven for two different and important functional groups.

Similar to birds, the visitation rates of terrestrial mammals were not affected by habitat complexity at the small spatial scale. However, mammal visitation rates increased with the proportion of suitable habitat at the large spatial scale. The higher visitation rates in extensively used landscapes may be the consequence of higher densities of roe deer (*Capreolus capreolus*

L.) and red fox (*Vulpes vulpes* L.) which were the most abundant visitors in these landscapes (Wilson and Mittermeier 2009; Grünewald et al. 2010). Another factor influencing the visitation rates could be differences in home range sizes between agricultural and forest landscapes (Börger et al. 2006). The distinct response of mammals to the gradient of landscape suitability suggests that the landscape features influencing movements and spatial distribution of mammal are differed from those affecting bees and birds. A possible explanation for that could again be related to behavioural differences: unlike bees and birds that are able to fly, mammals cannot avoid unfavourable habitat simply by overflying it; that is why wild boar (*Sus scrofa* L.), badgers (*Meles meles* L.) and martens (*Martes* spp.) which are associated with vegetation cover preferably move along hedges in structurally simple landscapes (MacDonald and Barrett 1993; Wilson and Mittermeier 2009). Our results demonstrate that in our model system different functional groups of animals respond in distinct ways to the same gradient in land-use intensity; thus, the differential responses were not due to differences in environmental context (Tylianakis et al. 2008b). Our findings rather suggest that different habitat requirements and foraging scales determine taxon-specific responses. Future studies should test whether such differences between functional groups of animals can be explained by specific species traits (see Bommarco et al. 2010).

In our model system, neither pollination success, measured as proportional fruit formation, nor seed dispersal, estimated by the number of removed cherries, was influenced by vegetation heterogeneity or landscape configuration. Thus, both ecosystem functions remained remarkably stable despite of the before mentioned changes in local species communities and visitation rates. Our results strongly suggest that for both pollination and seed-dispersal interactions the high mobility of animal pollinators and seed dispersers can compensate for changes in the corresponding species community and thereby buffer ecosystem functioning. This is an important finding because it shows that similar mechanisms may buffer ecosystem functions provided by highly mobile functional groups. Our findings are consistent with the hypothesis that changes in animal behaviour are more important than changes in species richness or abundance for ecosystem services produced by mobile organisms (Kremen et al. 2007).

Conclusions

In this study, we show that different functional groups of animals have distinct needs and habitat requirements and therefore respond very differently to the same gradient in vegetation complexity and landscape structure. Owing to the differential responses of the functional groups, different types of ecosystem processes, such as pollination and seed dispersal, can respond differently to the same gradient of human disturbance. In our model system, however, we found that both pollination success and seed-removal rates were surprisingly robust to changes in habitat and landscape structure although species richness and visitation rates of the corresponding functional groups did respond to the gradient in land-use intensity. This shows that changes in foraging distances can buffer pollination and seed-dispersal interactions in highly mobile animal taxa, such as bees and birds. Overall, our study highlights that it is not sufficient to measure the species richness or the interaction frequency of pollinator or seed-disperser species to understand the ultimate consequences for the corresponding ecosystem function. Future studies quantifying the impacts of human disturbance on ecosystem functions should therefore also look at behavioural changes of pollinator and disperser species in response to human disturbance.

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Chapter 5

Reduced seed-dispersal distances are congruent with low recruitment success in farmland populations of bird-dispersed cherry trees.

Abstract

1. In Central Europe, plant populations are patchily distributed in human-modified landscapes that comprise patches of semi-natural habitats within an agricultural matrix. To move from one population to another, many woody plant species depend on animal vectors. To assess the quality of animal seed dispersal in such landscapes, we compared the movement behaviour of an abundant bird seed disperser between semi-natural and agriculturally-dominated habitats and tested whether changes in animal movement behaviour affected seedling recruitment.

2. We performed feeding trials with wild cherries (*Prunus avium* L.) and Common Blackbirds (*Turdus merula* L.) to determine the distribution of regurgitation times. We captured 32 male blackbirds and equipped them with radio tags to follow their movements in forest and farmland habitats. To simulate the movement of cherry seeds through the landscape, we combined the distribution of regurgitation times with bird movement data and determined seed-dispersal distances and locations of seed deposition for forest and farmland birds.

3. According to our simulations, more cherry seeds were deposited under foraging trees in farmland (20.8 %) than in forest populations (9.5 %). Median seed-dispersal distances (50.8 m vs. 68.2 m) and the proportion of long-distance dispersal events (distances > 100 m) were lower in farmland (14.9 %) than in forest populations (28.2 %).

4. Forest-dwelling blackbirds dispersed more cherry seeds into suitable habitat (98.7 %) than farmland blackbirds (85.4 %). In both habitats, seed deposition in suitable habitat was much higher than expected from the proportion of suitable habitat within blackbirds' home ranges, indicating directed dispersal.

5. To test whether differences in seed-dispersal quality affected seedling recruitment, we recorded seedling densities in farmland and forest populations and determined survival

probabilities of seedlings. Seedling establishment and survival were much lower in farmland than in forest populations.

6. *Synthesis*: Our findings show for the first time that behavioural changes of animal seed dispersers can translate directly into differences in plant population dynamics. Although few cherry seeds appear to be dispersed into unsuitable habitats in farmland habitats, cherry populations in the farmland are prone to extinction because of short dispersal distances and subsequently low recruitment success.

Keywords: Animal movement, Ecosystem function, Land-use intensity Mutualism, Plant-animal interactions, *Prunus avium* L., Seed dispersal, Seedling recruitment, *Turdus merula* L., VHF radio telemetry

Introduction

Human-modified landscapes dominate most terrestrial ecosystems around the globe (MEA 2005a; Tylianakis et al. 2008a). In temperate regions, human land-use intensification has been particularly strong and agricultural landscapes have experienced substantial modifications due to the industrialisation of cultivation practices (Foley et al. 2005; MEA 2005a; UNEP 2007). These processes have created isolated patches of semi-natural habitats within a highly modified agricultural matrix, which has important consequences for the dynamics of plant (Cain et al. 2000; García and Chacoff 2007) and animal populations (Howe and Miriti 2004; Tylianakis et al. 2007).

One important consequence is that plant populations in intensively used landscapes are usually patchily distributed (Franzén and Nilsson 2010). Hence, plant propagules have to move large distances to reach other populations or to establish populations in new locations (Cain et al. 2000; Nathan 2006). Many plants depend on animal vectors for the movement of their seeds (Herrera 2002; Levey et al. 2005, Jordano et al. 2011). Frugivorous birds belong to the most important animal seed dispersers for plants with fleshy fruits (Snow and Snow 1988; Herrera 2002). They can displace seeds over long distances, can cross unfavourable habitats in flight and thereby efficiently interconnect isolated plant populations (e.g. García et al. 2010; Zamora et al. 2010). Hence, birds can act as "mobile links" between plant populations and have the potential to maintain seed-dispersal services for plants with fleshy fruits in human-modified landscapes (Lundberg and Moberg 2003; Price 2006; Kremen et al. 2007; Breitbach et al. 2010). Previous studies have even found that flight and thus dispersal distances were longer in highly modified structurally simple landscapes than in near-natural forest-dominated landscapes (Holbrook and Smith 2000; Gómez 2003; Lenz et al. 2011).

So far, many studies have investigated seed dispersal only in terms of dispersal distance (e.g. Holbrook and Smith 2000; Westcott and Graham 2000; Westcott et al. 2005; Lenz et al. 2011). However, from the plants’ perspective it is not only important how far seeds get dispersed but also where seeds are finally deposited, i.e. the quality of seed dispersal matters.

The quality of seed dispersal crucially depends on movement patterns of the dispersing animal vectors (Jordano et al. 2007; Spiegel and Nathan 2007). The "Directed Dispersal Hypothesis" (*sensu* Howe and Smallwood 1982) predicts that many animal vectors increase the probability that seeds are transferred to sites with suitable habitat conditions for plant recruitment. It follows from this hypothesis that directed dispersal is particularly important in human-modified landscapes where suitable habitats are patchily distributed (Cain et al. 2000; García and Chacoff 2007) and where many seeds are thus prone to fall into the unsuitable habitat matrix (Schupp 1993; Cain et al. 2000; Nathan 2006; Schurr et al. 2008). Consequently, seed dispersal quality is expected to be lower in landscapes where suitable habitats are patchily distributed, such as farmlands, than in homogeneous landscapes, such as forests (Dunford and Freemark 2004; Westcott et al. 2005; García et al. 2010).

A valuable approach to assess how seed dispersal services by birds change along a land-use gradient is to combine movement data of animal dispersal vectors, e.g. from radio tracking, with their gut retention times of seeds (Westcott et al. 2005; Lenz et al. 2011). However, previous studies using this approach did not incorporate the habitat requirements of the studied plant species into their model and thus were unable to predict seed fate after dispersal, i.e. the success of seedling recruitment (Westcott and Graham 2000; Gómez 2003; Westcott et al. 2005; Spiegel and Nathan 2007; García et al. 2010; Lenz et al. 2011). Hence, there is a lack of studies that have directly linked patterns of seed deposition with recruitment success, i.e. seedling establishment and survival (but see McConkey and Brockelman 2011), and we therefore know very little about the quality of seed dispersal by birds in human-modified landscapes (Schupp et al. 2010).

In this study, we examined seed-dispersal distances and quality of a widespread and bird-dispersed tree species (wild cherry, *Prunus avium* L.) in a human-modified landscape in Central Europe. The study area is dominated by agricultural land use and represents a typical human-modified landscape with high proportions of farmland interspersed with forests of various sizes; it is therefore well suited for the comparison of seed-dispersal distances and quality between cherry trees growing in forest and farmland habitats. While a previous study found that birds remove wild cherry seeds at similarly high frequencies in forest and farmland habitats (Breitbach et al. 2010), we do not know whether the actual seed-dispersal services of the birds change along the forest-farmland gradient. In forest and farmland, we therefore analysed the movement patterns of the Common Blackbird (*Turdus merula* L.) that is the most widespread and important seed disperser of wild cherry trees (Snow and Snow 1988; Breitbach et al. 2010). We combined movement data of blackbirds with regurgitation times of wild cherry seeds and determined dispersal distances for cherry seeds in forest and farmland habitats. In addition, we determined seed-dispersal quality by testing in which habitats seeds were more likely to be deposited and by recording seedling recruitment and mortality of wild cherries in forest and farmland habitats. We tested the following hypotheses: 1. Seed-dispersal distances are longer in the farmland than in the forest because of longer flight distances of blackbirds in the farmland. 2. Dispersal quality, i.e. the proportion of seed deposition in suitable habitat, is higher in forest than in farmland habitats where suitable habitats are more patchily distributed. To test whether these potential differences in seed dispersal influenced recruitment success, we compared seedling recruitment between forest and farmland.

Materials and methods

Study region

Our study region is located in Rhineland-Palatinate (49°38’N–49°58’N, 7°45’E–8°22’E) in Central Germany and covers approximately 1,900 km^2 (Fig. 5.1). Surrounded by mountain ranges in the northwest (Hunsrück, Taunus) and southwest (Donnersberg), the region belongs to one of the warmest and driest parts of Central Europe (mean [annual] temperature: ~10.0 °C; average rainfall: 500 mm; Ambos & Kandler 1987). Owing to the topographical position amidst mountain ranges and its stable climatic conditions, the landscape is intensely used for agriculture (grain, wine, rapeseed, vegetables and some pomiculture), interspersed with patches of semi-natural habitat such as transitional woodland-shrub, pastures, natural grasslands and sparsely vegetated areas. The boardering mountain ranges are covered with mixed deciduous forest.

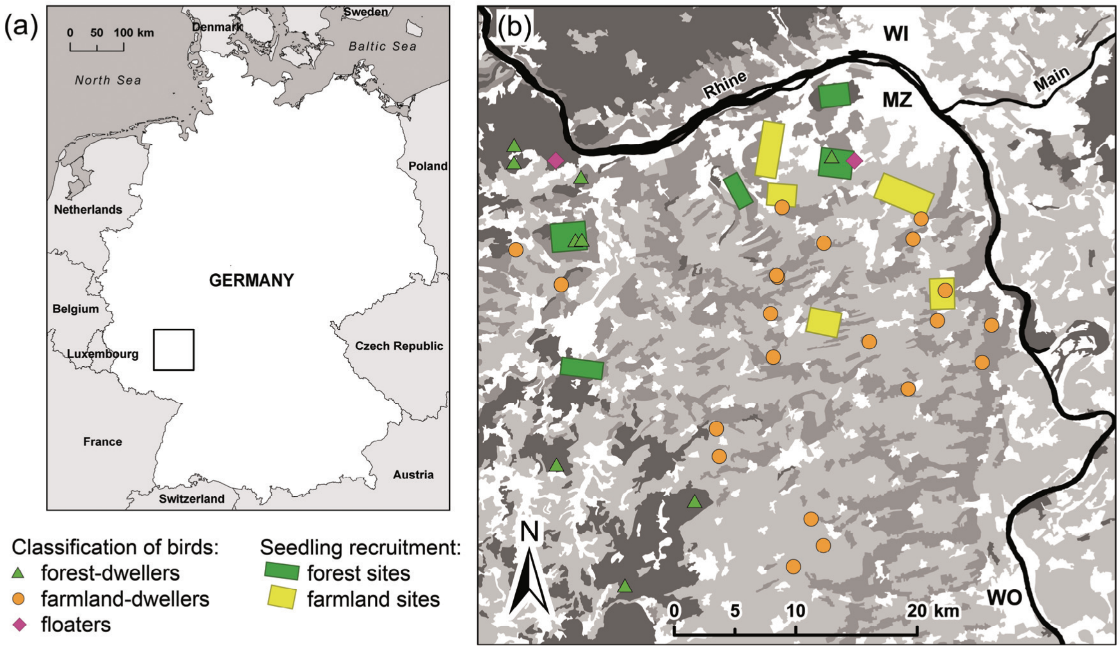

Figure 5.1: Map of the study area: **(a)** Location and dimension of the study area in central Germany, indicated by a *square*. **(b)** The location of 32 Common Blackbirds in the study area. Courses of main rivers are shown in *black* (i.e. Rhine and Main); bigger cities abbreviated as WI (Wiesbaden), MZ (Mainz) and WO (Worms). Also shown are forests (*dark grey shaded areas*), viniculture and pomiculture (*middle grey shaded areas*) and structurally simple agricultural landscapes (*light grey shaded areas*).

Study species

The wild cherry, *Prunus avium* L. (Rosaceae), is widespread throughout Europe and inhabits a wide range of different habitats including deciduous mixed forest, forest edges, small woods, hedgerows and fallows. *P. avium* is a small deciduous tree growing up to 15–20 m (rarely 30 m) in height. Early flowering in April and May is followed by an early fruiting period which lasts from June to August (Breitbach et al. 2010; Breitbach et al. 2012). The fruits consist of a fleshy mesocarp which turns from green to glossy black during ripening and a single seed encased in a wooden endocarp (i.e. a drupe). Fruits are roundish with a diameter of 14.7 ± 2.2 mm (mean ± 1 SD, *N* = 1,674) and weigh 2.0 ± 1.0 g (mean ± 1 SD, *N* = 1,674). Ripe cherries are consumed and thus dispersed by a variety of animals, in particular by birds and mammals (Breitbach et al. 2010; Grünewald et al. 2010). Seeds of wild cherry trees require winter stratification and germinate in the spring of the following year prior to foliation of deciduous trees (Suszka et al. 1996).

The Common Blackbird (*Turdus merula* L., blackbird hereafter) is the most numerous and widespread member of the Thrush family in Central Europe (Bauer et al. 2005). The species is the most versatile frugivore among the European thrushes and also the main disperser of wild cherry seeds in our study area (Breitbach et al. 2010). Through successful adaptation to human altered landscapes, blackbirds nowadays inhabit a wide range of different habitat types from dense forest, woodland, structurally complex to structurally simple agricultural landscapes and urban areas. However, behaviour and habitat use differ among individuals that inhabit either forest or farmland; the two groups dwelling in these two habitat categories are therefore often considered as distinct populations (Haffer 1988; Stephan 1999; Bauer et al. 2005). We chose only male birds for our study since most females breed during the fruiting period of the wild cherry and therefore do not move very much. Male blackbirds hold territories in which they actively move around, for instance to defend territories against conspecifics and to collect food for their offspring; male blackbirds can therefore be considered as more important seed dispersal agents for wild cherry trees than female blackbirds.

We chose *P. avium* and *T. merula* because both species are reasonably common in the study area and are very widespread in Central Europe. Moreover, both species are found in a wide range of habitat types with varying intensity of human land use (Breitbach et al. 2010; Breitbach et al. 2012). Thus, the cherry-blackbird system is a very well-suited study system to investigate the seed-dispersal interactions between plants and animals in human-modified landscapes in Central Europe.

Feeding trials

We captured 15 adult male blackbirds using standard mist-nets (R. Vohwinkel, Velbert, Germany) at the University Campus in Mainz in early summer of 2009 and 2010. All birds were weighted, measured and ringed according to the standards of the responsible authorities (Vogelwarte Radolfzell and EURING). All birds were individually marked with a unique combination of three colour rings. The birds were held separately in cages of 1 × 1 × 2 m (length × width × height). We performed feeding trials with all captured birds using ripe wild cherries from trees within our study area. Feeding trials lasted from sunrise to sunset but were paused during noon where blackbirds exhibit a very low feeding activity (Breitbach et al. 2010). Blackbirds swallow wild cherry drupes as a whole and a clean seed is later regurgitated. Thus, wild cherry fruits, unlike smaller fruits, do not pass through the birds' gut and are very unlikely to be regurgitated while in flight. For a clear detection of regurgitated seeds, we placed fresh light-coloured blotting paper on the ground of the cages before each feeding trial started. All birds had access to food (fat-enriched bird food, mealworms, other fruits) and water throughout the feeding trials. Individual birds were observed from a hidden position in some distance from the cages. To be able to determine the exact regurgitation time (RT) for a particular seed, we offered only one cherry drupe per feeding trial. For each feeding trial, we calculated the RT as the timespan from the time of ingestion to the time of regurgitation, i.e. when the seed dropped to the blotting paper. Across all feeding trials ($N = 63$), we fitted an average RT distribution (function *density* in R) with a bandwidth of 5 minutes as smoothing factor, i.e. we fitted a function which enabled us to predict the proportion of seeds that were regurgitated during one-minute intervals within the range of observed regurgitation times (see Fig. A7.1, Appendix 7).

Radio tracking and movement analysis

We caught 32 adult male blackbirds with mist-nets across the entire study area (Fig. 5.1) in two consecutive field seasons from 18.06. to 24.07.2008 (8 birds) and from 01.06. to 24.07.2009 (24 birds). All birds were individually marked with a unique combination of three colour rings to allow reliable visual identification of each bird in the field. We supplied all birds with VHF radio tags (PIP3, Biotrack Ltd., Wareham, UK) using the leg-loop harness method described in Rappole and Tipton (1990) for fixation with leg-loop lengths derived from Naef-Daenzer (2007). The average tag weight of 2.3 g (total payload = 2.6 g, for tag incl. harness and all rings together) was well below the threshold of 5 % of the birds' body mass (Kenward 2001) (body weight: mean = 90.1 g, range = 79.8–99.1 g; payload as percentage of body mass: mean = 2.89 %, range = 2.58–3.38 %; *N* = 32). We used single filaments of braided rubber ropes (Mamutec AG, St. Gallen, Switzerland) as leg-loops, allowing tags to fall off after about 12 weeks due to gradual disintegration of the rubber. We never observed that birds were bothered by radio tags during tracking times. Nevertheless, we started radio tracking one week after birds had been captured so that birds were able to adapt to the tag before radio tracking started.

To exactly locate the study birds, we used terrestrial VHF radio tracking during two successive fruiting seasons of the wild cherry. We followed the study birds from sunrise to sunset for continuous periods as often and as good as possible. During bird-tracking, we recorded a new location (i.e. the exact geographic position) whenever we recognised a change in the birds' position – either visually, acoustically (i.e. bird song or call) or by changes in the position of the transmitter signal. Our aim was to obtain intervisibility with the bird as often as possible to clearly identify the individual through its colour rings or the mounted tag. In cases without intervisibility, we used the antenna to estimate a bird's location from signal strength and direction. To record the location of the bird, we then used one of the following methods: **1) from a distance** – First, we recorded the observer position using a handheld GPS receiver (Garmin eTrex Vista HCx). Second, we took a bearing by pointing a compass (Recta DS 50) towards the position of the bird. Finally, we determined the distance from the observer to the birds' position using a laser range finder (LRF; Nikon Laser800). The true location of the bird was later computed using the function *gcDestination* from the R package *maptools* with these three indirect measures as input variables (observer position, bearing and distance to bird). **2) direct location** – After the bird left a position we moved to that position and the location using the GPS receiver; this resulted in a direct fix. **3) known positions** – After some days, every observer was able to recognise favourite places of the tagged birds (e.g. nest site, songpost, etc.); these positions were stored in the GPS receivers and were reused as location. **4) map positions** – A further method that was used in some occasions was to identify and to mark the position on fine scale maps. The exact location was identified later using Google Earth or

ArcMap. With these methods, we obtained the location of each individual bird with a temporal resolution of one minute which resulted in a total of 103,742 fixes with known geographic positions for all 32 birds.

In the lab, we determined the habitat type at the position of all locations. To account for the inaccuracy of the GPS receivers in the field, we placed buffer zones of 10 m radius around the coordinate of each location. Within each buffer we identified habitat types by using GIS software (ArcINFO v. 10.0, ESRI) and digital land-use data from our study area (ATKIS Basis-DLM, Landesamt für Vermessung und Geobasisinformation Rheinland-Pfalz, Koblenz, Germany). The ATKIS data represent the most up-to-date and fine-scaled vector maps of habitat types in our study area and yield a high spatial resolution (± 3 m). We added missing information to the ATKIS data, for instance narrow hedgerows or small woods in structurally simple landscapes. We used the information of habitat type inside the buffer of each location to determine the availability of suitable habitats for wild cherry trees. Suitable habitat types included: broad-leaved and mixed forests (*not* coniferous forests), woods, woodland shrub, hedgerows and green belts at road verges (see Table A8.1, Appendix 8). All bird locations that included one of the suitable habitat types were classified as suitable locations for wild cherries, all others as unsuitable.

Dispersal curve estimation

We combined the distribution of regurgitation times (Fig. A7.1, Appendix 7) and the bird movement data to estimate the movement paths of cherry seeds through the landscape. To do so, we drew 10,000 time intervals from the RT distribution curve in one-minute steps (with replacement). For instance, a RT of 30 minutes had a probability of 3.52 % and was therefore 352 times included within the total of 10,000 regurgitation times (Table A7.2, Appendix 7). To estimate the movement distances of a bird during each of the 10,000 regurgitation times, we drew 10,000 starting points from the movement data of each individual bird, determined the bird's location at the time of regurgitation and estimated the distance between the starting point and the location of regurgitation; note that this distance is not the movement distance of a bird but the distance between the ingestion and regurgitation location, e.g. a moving bird that returns to the starting point for regurgitation provides a dispersal distance of 0 m. To draw the starting points, we combined the locations of all tracking days of an individual bird; these data represent the movement behavior of each individual bird throughout the study period. Because we aimed at virtually tracking the dispersal of wild cherry seeds, we defined that seed-dispersal events could only start in habitat types where wild cherry trees are able to grow. Hence, only bird locations within suitable habitats for wild cherries were valid starting points. With this procedure, we obtained 10,000 dispersal distances per bird individual (320,000 dispersal distances in total) with each bird movement starting in suitable wild cherry habitat. For each individual bird, we used these data to calculate the distribution of dispersal distances (Fig. A9.1, Appendix 9). For simplicity, we divided dispersal distances into evenly distributed distance classes on a logarithmic scale (i.e. 0.2 units on a log10(x + 1)-scale) and calculated the mean percentage of seed dispersal events (± 1 SE) in each distance class.

Average seed dispersal – We combined the individual dispersal distributions into one distribution of seed-dispersal distances averaged across all 32 blackbird individuals. The number of tracking days per individual bird, i.e. bursts, ranged from one to 11 days with 1.7 hours for the shortest burst and 16.6 hours for the longest burst. To account for the different number of locations among bird individuals and thus for differences in the accuracy of the estimation of bird movement behaviour, we weighted individuals by the number of fixes, i.e. weighted by the log10 of the total number of locations of an individual. Birds with more locations were thus given more weight compared to birds with a lower number of locations. This procedure resulted in an overall seed dispersal distribution for our study area. To additionally assess the quality of seed dispersal for the wild cherry, we split the distribution of seed dispersal distances into a) dispersal events into suitable habitats for the wild cherry and b) dispersal events into unsuitable habitat. We did this for each bird individual separately and then averaged across all bird individuals.

Habitat-specific seed dispersal – We compared seed dispersal by blackbirds between natural forest habitats and the human-altered open landscape (i.e. farmland). We therefore classified the 32 bird individuals as either forest-dwelling birds or as inhabitants of farmland. To do so, we identified the ATKIS categories that belong to forest or to farmland (Table A8.2, Appendix 8) and calculated for each bird individual how frequently a bird was located in forest or in farmland habitats, i.e. how many locations were recorded within the respective landscape type.

After the classification of birds, we only allowed starting points of seed-dispersal events that were situated in the respective habitat type, i.e. forest birds only dispersed cherry trees growing in the forest and vice versa. We then used the same procedure as described above to estimate the distributions of seed dispersal distances for blackbirds of forest and farmland and estimated the proportion of seeds that were deposited into either suitable or unsuitable habitats. We compared whether the proportion of regurgitation events directly at the foraging tree, i.e. null-dispersal events, differed between forest and farmland birds with a two-sided Wilcoxon signed rank tests. Additionally, we compared median dispersal distances between blackbirds in forests and in farmland. To further assess the quality of seed dispersal for forest and farmland, we defined long-distance dispersal as dispersal events reaching > 100 m from the foraging tree (*sensu* Cain et al. 2000) and determined the proportion of these events for each blackbird. We then compared the proportions of long-distance dispersal events between forest and farmland and also tested for differences in the maximum seed-dispersal distances between the two habitat types.

Finally, we compared the predicted proportion of seed-dispersal events into suitable versus unsuitable habitat types with the present distribution of suitable and unsuitable habitat types within the home range of each bird individual. This additional analysis aimed at testing whether blackbirds dispersed cherry seeds directed into suitable habitats or distribute seeds randomly across all habitat types within their home ranges. To do so, we first calculated 100 % Minimum Convex Polygons (MCPs) and the corresponding areas from the locations of each individual bird separately using the function *mcp* included in the *adehabitatHR* package. We then used ArcINFO to determine the proportions of suitable and unsuitable habitat inside each MCP through intersection with the ATKIS data. For blackbirds in forest and farmland, we then tested whether the proportion of suitable habitat for wild cherry trees within the home range of a bird differed from the proportion of predicted dispersal events into suitable cherry habitat.

Seedling establishment and survival

In 2009, we selected five sites in forest habitats (at least 50 m from the forest edge) and five farmland sites, i.e. hedgerows and small woods, with wild cherry populations (Fig. 5.1b). At each site, we established five study plots that had a pair-wise distance of at least 150 m. Study plots cut through a cherry population and were 100 m long and 2 m wide (plot size 200 m²). Within each plot, we counted all cherry seedlings at the beginning and in the middle of April, i.e. when cherry seedlings appeared on the forest floor. Cherry seedlings are readily identified by the shape of their first leaves and were distinguished from cherry saplings or clonal offspring by the presence of cotyledons. The number of seedlings at the first and the second count were closely correlated ($N = 50$, $r = 0.98$, $P < 0.001$). We therefore only compared the number of seedlings during the second census between forest and farmland sites. To do so, we first averaged the number of cherry seedlings across study plots per site, then log10-transformed the number of seedlings per plot and finally compared seedling densities between forest and farmland sites with an ANOVA.

To assess whether seedling survival differed between forest and farmland, we selected at each site the study plot with the highest number of established seedlings and individually marked all cherry seedlings within the respective plot with straw rings and numbered tags in mid April. At sites with many seedlings, we did not mark all of them but randomly selected 20 seedlings; the number of marked seedlings per site ranged from 4 to 20 seedlings. We followed the fate of these seedlings until mid June in two-week intervals and checked at each census whether a seedling was still alive. To estimate the probability of seedling survival for each site, we determined the proportion of marked seedlings that had survived the entire census period until mid June. This survival rate is a good proxy of first-year seedling survival because the mortality of cherry seedlings from June to September was very low in a previous study (M. Schleuning, unpublished data). We compared seedling survival between forest and farmland sites with an ANOVA; transformation of seedling survival was not necessary because the residuals were normally distributed and variances were homogeneous.

Results

Feeding trials

Regurgitation times of cherry seeds in 63 feeding trials ranged from 8 to 98 minutes with a median of 29.6 minutes over all feeding trials (Fig. A7.1, Appendix 7). The distribution of RTs is leptokurtic with a peak at around 29 minutes and a fat tail to the right.

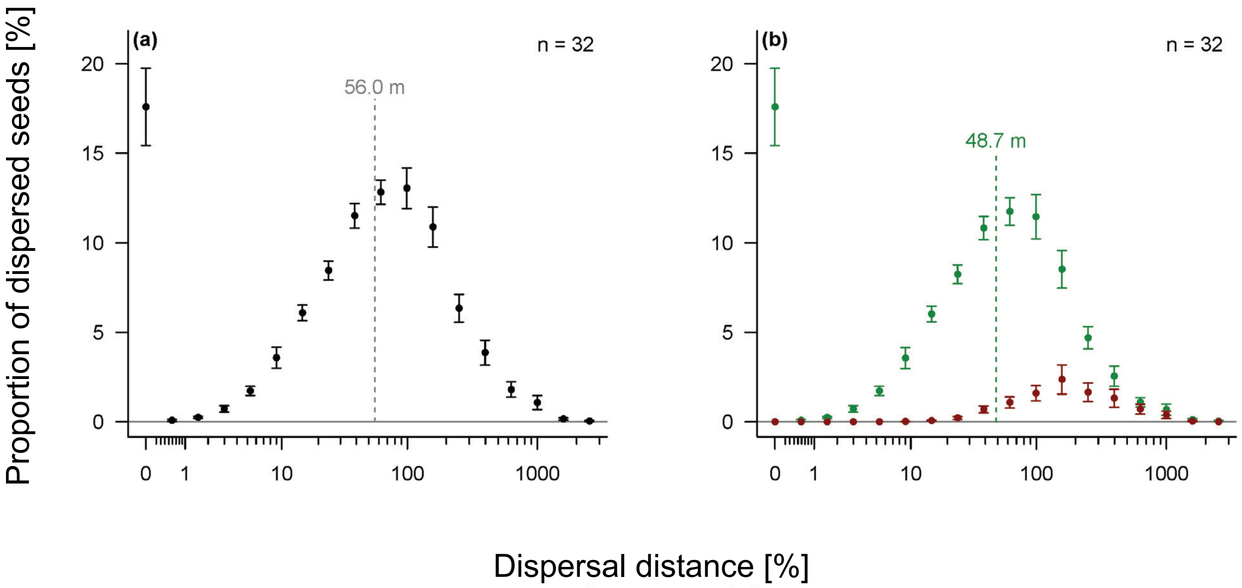

Figure 5.2: Predicted seed-dispersal distances (SDDs) for the cherry-blackbird system. **(a)** Overall SDDs averaged over all 32 blackbird individuals (± 1 SE). **(b)** SDDs of (a) were split into seed-dispersal events into suitable habitat for the wild cherry (*green curve*) or unsuitable habitat (*red curve*). For each curve the median of the SDD is indicated (*dashed line*). Note the high proportion of seeds that were not dispersed away from the place of origin (i.e. null-dispersal events) at the left-hand side of each distribution.

Overall distribution of seed-dispersal distances

A considerable number of seeds (mean = 17.6 %, range = 2.3–59.1 %) were deposited directly at the foraging tree and were thus not dispersed (null-dispersal, i.e. dispersal events with dispersal distance = 0 m; Fig. 5.2a). The median seed-dispersal distances ranged from 11.4 to 133.4 m among the 32 blackbird individuals (see Fig. A9.1, Appendix 9). Overall, 28.2 % (range: 5.9–60.0 %) of seeds were dispersed to a distance of > 100 m away from the foraging tree. The maximum seed dispersal distance of a single bird individual was 2,220 m. The proportion of seeds deposited in suitable habitat for the wild cherry was 89.9 % (Fig. 5.2b). The deposition in unsuitable habitat was negligibly small at dispersal distances < 50 m and was relatively more important at large distances. Nevertheless, the proportions of seeds that were dispersed into suitable habitat were always higher than those dispersed into unsuitable habitat.

Habitat preferences of blackbirds

Most birds showed pronounced habitat preferences for either forest or farmland. In nine blackbirds, more than 85 % of their locations came from forest habitats, whereas in 21 birds more than 80% of their locations were recorded in farmland (Table A10.3, Appendix 10). Only two birds were recorded with similar frequencies in forest and farmland habitats (Table A10.3, Appendix 10), and we therefore excluded these two bird individuals from the analysis of habitat-specific seed-dispersal. Hence, for the following analyses, 9 blackbirds were classified as forest birds (87,598 predicted dispersal distances) and 21 blackbirds were birds predominantly foraging in farmland (204,270 predicted dispersal distances).

Habitat-specific seed-dispersal distances

In both forest and in farmland, a rather high proportion of cherry seeds were not dispersed away from the foraging tree (forest: 9.5 %; farmland: 20.8 %). Null-dispersal was significantly more frequent in the farmland than in the forest (unpaired Wilcoxon-test: $W = 41$, $P = 0.014$). In contrast to our hypothesis, blackbirds in forest dispersed seeds over longer distances than birds in farmland. Even when neglecting null-dispersal events, median dispersal distances were significantly higher in the forest (68.2 m) than in farmland (50.8 m; unpaired Wilcoxon-test: $W = 153$, $P = 0.007$). The proportion of long-distance seed-dispersal events (> 100 m) was twice as high in forest (28.2 %) than in farmland habitats (14.9 %; unpaired Wilcoxon-test: $W = 163$, $P =$

0.001). However, the predicted maximum seed-dispersal distances for forest (774.0 m) and for farmland (998.8 m) birds did not differ between the two habitat types (unpaired Wilcoxon-test: *W* = 72, *P* = 0.326).

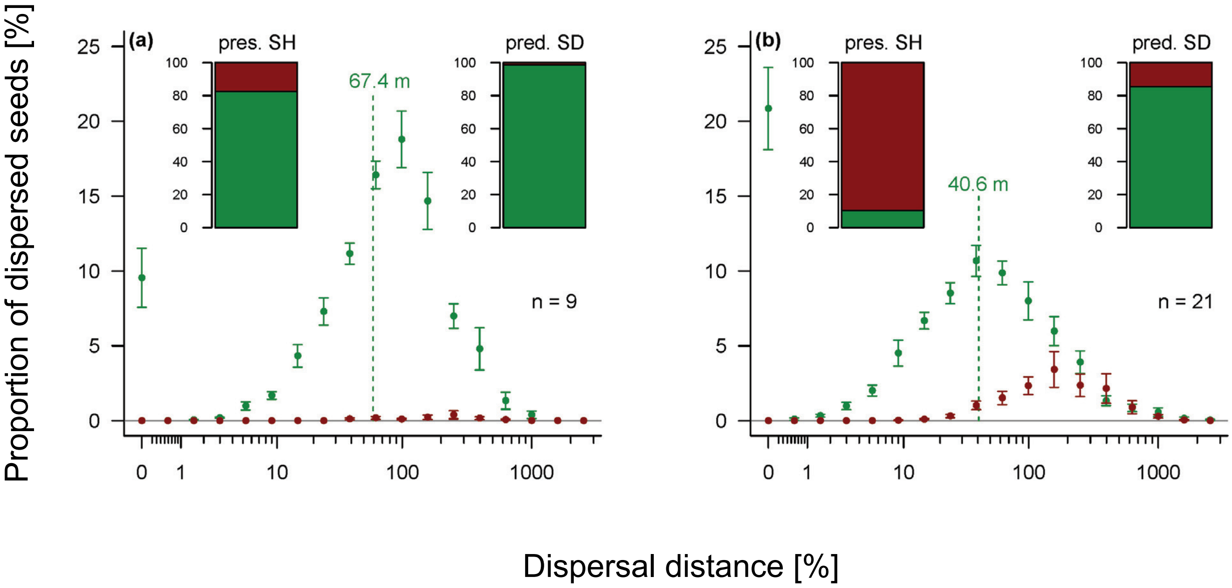

Figure 5.3: Seed-dispersal distributions (SDDs) and directed-dispersal capacity (*barplots*) for Common Blackbirds in forest and farmland habitats. SDDs and the difference between the proportion of present suitable habitat (*pres. SH*; in %) and predicted seed dispersal (*pred. SD*; in %) **(a)** in the forest (*n* = 9 forest-dwelling blackbirds) and **(b)** in the farmland (*n* = 21 farmland-dwelling blackbirds). For each SDD curve, the predicted SDDs (± 1 SE) into suitable (*green*) and unsuitable (*red*) habitat for wild cherries are given. For each curve, the median of the SDD is indicated (*dashed line*).

Directed dispersal in forest and farmland

Forest-dwelling blackbirds dispersed almost all cherry seeds into suitable habitat (98.7 %), whereas blackbirds that inhabit farmland sites deposited a significantly smaller proportion of seeds into suitable habitat (85.4 %; unpaired Wilcoxon-test: *W* = 168, *P* < 0.001). We compared these predicted proportions with the proportion of suitable habitats that are present within the home ranges of blackbirds in the forest and in the farmland. Present suitable habitat types, i.e. potential habitats for wild cherries, accounted for 82.5 % of habitat types within home ranges of forest-dwelling blackbirds compared to a much lower proportion of only 9.8 % for blackbirds that inhabit farmland (*W* = 189, *P* < 0.001; Fig. 5.3a,b left bars). In both habitat types, the predicted seed deposition in suitable habitat was much higher than would be expected from the overall present proportion of suitable habitat (paired Wilcoxon-tests: forest: $V = 45$, $P < 0.004$, Fig. 5.3a bars; farmland: $V = 231$, $P < 0.001$, Fig. 5.3b bars), indicating that seeds were not randomly but distributed directed within the home range of a blackbird.

Seedling establishment and survival

We tested whether the higher quality of seed-dispersal by blackbirds in forest than in farmland habitats was consistent with the observed patterns in seedling recruitment. Consistent with these findings, the number of established seedlings at the beginning of the growing season was almost three times as high in forest than in farmland habitats ($F_{1,8} = 14.0$, $P = 0.006$; Fig. 5.4a). Moreover, seedling survival during the establishment process, i.e. from April to June, was more than twice as high in forest than in farmland populations ($F = 18.8$, $P = 0.002$; Fig. 5.4b).

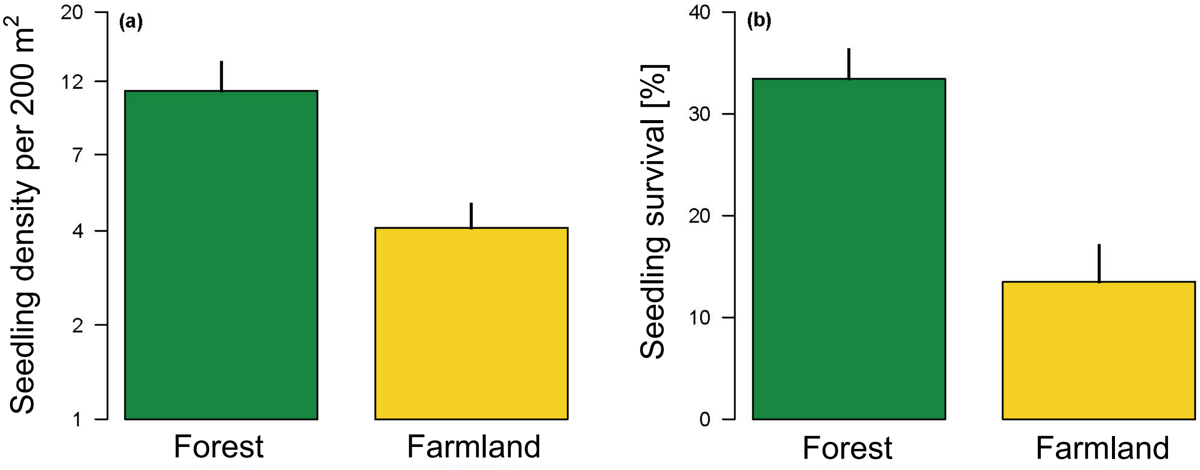

Figure 5.4: Seedling density and survival of wild cherries at five sites in forest habitat (*green bar*) and at five sites in farmland habitat (*yellow bar*). **(a)** The mean number of cherry seedlings per 200 m^2 in April 2009 (± 1 SE); note log10-scale of seedling density. **(b)** The probability of survival (± 1 SE) of individually marked seedlings from April to June 2009 at the same sites.

Discussion

Seed-dispersal distances

Blackbirds dispersed wild cherry seeds differently in forest and farmland habitats. These results are consistent with the findings of previous studies that showed that movement patterns of birds change along habitat gradients in human-modified landscapes (e.g. Gómez 2003; Spiegel and Nathan 2007; Lenz et al. 2011). Most previous studies found that movement and dispersal distances increased in structurally simple landscapes (Graham 2001; Gómez 2003; Nathan et al. 2008; Lenz et al. 2011). In the cherry-blackbird system, we found, however, shorter median seed-dispersal distances and less long-distance dispersal events in farmland than in forest. A likely explanation for this surprising pattern could be the territorial behaviour of blackbirds and smaller territory sizes in farmland than in forest landscapes (Niggemann et al., submitted) because food sources, e.g. fruiting trees, are highly aggregated in the farmland, for instance in small hedgerows. In contrast, resources are more sparsely distributed in the forest (Breitbach et al. 2012). Simulation models of bird movements also predicted that dispersal distances decrease with the spatial aggregation of fruit resources (Morales and Carlo 2006). In our system, another important difference in seed-dispersal services between forest and farmland was that null-dispersal events were more likely in farmland than in forest habitats. Like most territorial bird species, blackbirds behave as central place foragers (*sensu* Orians and Pearson 1979) and frequently return to central places such as the preferred foraging sites. This behaviour could explain why, according to our simulations, so many seeds were deposited at the foraging site. Since the central places of most bird species are located within micro-habitats of high woody plant cover (Jordano et al. 2007; Breitbach et al. 2010) and since these habitat structures are limited in the farmland habitat, farmland blackbirds frequently return to the same location. In contrast, forest birds are less bound to specific habitat structures, move less directed through their territories and thereby cover longer distances (Niggemann et al., submitted).

Our findings indicate that changes in bird-mediated seed-dispersal services from structurally rich to structurally poor habitats, e.g. from forest to farmland, strongly depend on the territoriality of the bird species and on changes in territory size from one habitat type to another. In contrast to our study, previous studies looked at movement patterns of less territorial bird species or non-breeding individuals (Holbrook and Smith 2000; Graham 2001; Gómez 2003; Holbrook 2011; Lenz et al. 2011). Their movement behaviour might be very different from highly territorial species. For instance, Sun et al. (1997) found that a non-territorial turaco species traverse an up to 20 times larger area than two territorial turaco species in an African forest ecosystem. Similar to non-territorial bird species, forest species that visit farmland trees occasionally disperse seeds over long distances because they move to foraging trees in the farmland and then return to their central places in forested habitats (Da Silva et al. 1996; Eshiamwata et al. 2006; Herrera and García 2009). Such floating bird individuals that frequently cross habitat borders are important for an exchange of plant seeds between plant populations (Pejchar et al. 2008; Herrera and García 2009). In the blackbird-cherry system, however, only two of 32 bird individuals frequently moved between forest and farmland habitats and according to our simulations only about 0.6 % of cherry seeds were transported from farmland into forest and vice versa. Despite the importance of floating bird individuals for long-distance dispersal (Lenz et al. 2011), abundant and territorial farmland birds remove more seeds (Breitbach et al. 2010) and thus are more important seed dispersers for farmland plants than floaters or non-breeding individuals. Thus, previous studies of bird individuals that were not territorial when the study was conducted may over-estimate seed-dispersal distances provided by birds.

Directed dispersal

In the farmland, less seeds reached suitable habitats than in the forest. Nevertheless, despite the very low proportions of suitable habitat in the farmland (9.8 %), blackbirds deposited the majority of cherry seeds in suitable habitats such as hedgerows and woodlots (85.4 %). This strong effect of directed dispersal is due to the fact that blackbirds prefer locations with high plant cover and avoid habitats such as croplands that are unsuitable for tree recruitment. In the forest, the effects of directed dispersal were even stronger and almost all cherry seeds (98.7 %) were deposited in suitable habitats although home ranges of blackbirds in the forest contained quite high proportions of unsuitable habitat, mostly coniferous forests (up to 17.5 % within blackbird home ranges). Our findings are consistent with previous studies showing that birds are excellent seed dispersers and may outperform other biotic seed-dispersal agent such as mammals (Sekercioglu 2006) as well as abiotic dispersal agents like wind and water (Fenner and Thompson 2005), in particular in terms of seed-dispersal quality. Blackbirds might be particularly good seed dispersers for cherries because regurgitation of cherry seeds was only observed in perched blackbirds. In contrast, larger bird species usually defecate seeds after gut passage, even those of large-sized fruits (Snow and Snow 1988; Lenz et al. 2011) which is also possible in flight. This difference between regurgitation and defecation has direct implications for the quality of seed dispersal, since regurgitation reduces the amount of seeds that are dropped en route, i.e. on the way from one patch of suitable habitat to another. Thus, species-specific handling of seeds contributes to more directed seed dispersal to suitable habitats. High rates of directed dispersal, also in other plant-bird dispersal systems, may explain why hedgerows and small woodlots have been identified as dispersal foci for fleshy-fruited trees in human-dominated landscapes (Pejchar et al. 2008; Herrera and García 2009).

Seedling recruitment

Establishment and survival of cherry seedlings was much higher in forest than in farmland populations. These differences in seedling recruitment are likely to be caused by differences in seed-dispersal quality between farmland and forest populations. A possible explanation is that a higher proportion of cherry seeds was deposited in unsuitable habitat in farmland than in forest. However, seed rain is similar in forest and farmland populations at our study sites (Breitbach et al. 2010). Therefore, it seems plausible that the differences in dispersal distances are the main determinant of the higher recruitment probabilities in forest than in farmland since establishment probabilities are higher for seeds that have been dispersed over longer distances (Nathan and Muller-Landau 2000). This is because seedling mortality is usually higher in the vicinity of parental plants because of higher densities of specialised pathogens and herbivores in dense conspecific stands (Janzen 1970; Connell 1971; Schupp et al. 2010). Farmland populations of wild cherries have very high adult densities, while trees grow more sparsely in forest habitats (Böhm 2009). Clumps in the farmland have often been formed by clonal propagation from root stocks after a site had been colonised (Fernandez et al. 1996). It seems likely that cherry seeds have to escape from such clumps because intra-specific competition with competitively superior clonal propagules can strongly reduce seedling recruitment in clonal plant populations (Schleuning et al. 2009). In our system, we additionally found that the proportion of damaged leaves, probably by fungi infections, increased with the density of adult cherry trees in a population (N = 10 populations, r = 0.69, P = 0.026; Böhm 2009). This indicates that density-dependent processes indeed affect seedling recruitment in wild cherry populations. Therefore, the low dispersal distances in the farmland that usually do not reach beyond a population may strongly contribute to low recruitment success of cherry seedlings in the dense farmland populations. Nevertheless, other differences between forest and farmland populations, e.g. in abiotic conditions, could also contribute to differences in seedling recruitment. One additional factor limiting seedling recruitment in farmland populations could be high nitrogen fertilisation from adjacent agricultural fields (Suding et al. 2005). Furthermore, potential differences in the genotypic diversity between forest and farmland populations could affect the establishment success of seedlings (Bischoff et al. 2010), in particular because many farmland populations originate from planted populations. Although we cannot rule out these additional factors, the consistent patterns in seed-dispersal distances and recruitment success indicate that recruitment probabilities of wild cherries are at least partly determined by the seed-dispersal services provided by blackbirds.

Caveats

The combination of movement data from mobile seed dispersers and their retention times provide reliable predictions of seed-dispersal distances and the locations of seed deposition (Wang and Smith 2002; Schupp et al. 2010). Although we predicted seed dispersal by using a simulation approach, we are confident that our predictions are closely related to seed-dispersal patterns in the real world because our simulations were based on a wealth of empirical data from the study area. Nevertheless, we only looked at a single, albeit very important seed disperser species. Because different dispersers species may deposit seeds differently in the landscape (Jordano et al. 2007), future studies should aim to cover a greater spectrum of disperser species, e.g. incorporate both bird and mammal dispersers. Similarly, our study looked at a single large-fruited plant species that fruits comparatively early in the year, at a time when most Central European birds are breeding (Bauer et al. 2005). Seed-dispersal patterns could be different in plant species with smaller fruits and later fruiting periods, for instance *Sambucus* spp. and *Crataegus* spp. In the future, studies that assess the outcome of seed-dispersal interactions between plants and mobile dispersal agents will become increasingly important (Westcott et al. 2005; Spiegel and Nathan 2007; Lenz et al. 2011), for example to predict the responses of plant populations to global change and for answering the question how fast plant populations could track their climatic niche (McLachlan et al. 2005; Pearson and Dawson 2005).

Conclusions

We found that blackbirds are highly efficient seed dispersers in temperate human-modified landscapes. Blackbirds deposit almost all wild cherry seeds into habitat that is potentially suitable for seedling establishment, almost independent of the suitability of the prevailing habitat matrix. Seed dispersal by birds is thus very valuable for plant species with patchy populations in human-modified landscapes and provides gene flow between isolated populations, at least occasionally. These findings emphasise that animal-mediated seed dispersal is an important ecosystem process, also in temperate ecosystems. Due to changes in movement behaviour, blackbirds dispersed wild cherry seeds in the farmland over shorter distances than in the forest leading to reduced recruitment success in farmland populations. These findings show for the first time that changes in the behaviour of animal seed dispersers can translate directly into differences in plant population dynamics. From a conservation perspective, we conclude that tree populations in the farmland are prone to extinction in the long term because of restricted seed exchange between populations and low levels of seedling recruitment.

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6 General Conclusions

Pollination and seed dispersal by animals are ecosystem functions that play a key role in the exchange of genetic material between plant populations. Pollination is crucial for plant reproductive success and contributes to the genetic exchange between populations which is essential for population viability and adaptive potential. Seed dispersal is necessary to circumvent density-dependent mortality of seeds and seedlings and enables plants to occupy suitable habitats and to found new populations. When investigating the relationship between ecosystem functions and anthropogenic changes in the spatial configuration of landscapes, it is important to investigate the involved processes comprehensively and to include all relevant life-cycle stages and interacting species. To assess the ultimate consequences of land-use change for plant reproductive success, we thus need to understand pollination as well as seed dispersal since both ecosystem functions contribute to plant reproduction. In my thesis, I investigated animal-mediated pollination and seed dispersal and the resulting seedling recruitment using the wild cherry (*Prunus avium*) in the human-modified landscapes of Rhineland-Palatinate in Central Germany as a model system.

6.1 Pollination

One major part of my thesis focused on the investigation of how pollination of wild cherry trees is affected by land-use intensification at two different spatial scales: specific habitat features (i.e. vertical vegetation heterogeneity) at a local scale (70 m radius) and changes in the landscape configuration at a large spatial scale (2,000 m radius). I aimed to assess the entire process of pollination from the visitation of flowers by pollinating insects up to the final seed set of wild cherry trees. First, I compared the responses of species richness of the local bee community, i.e. in a radius of 20 m around each target tree, between the local and the landscape scale. Next, I compared the response of flower visitation rates of pollinators between the small and the large spatial scale. At last, I tested how the final output of the pollination function, i.e. pollination success, was affected by land-use and by the local bee species richness. For the local bee community, species richness was only influenced by land-use at the small spatial scale and increased in open habitats. This reflects the preference of wild bees for open habitat structures (Westrich 1989a) where the chances to find suitable nesting sites are highest (Westrich 1989b; Schmid-Egger et al. 1995; Westrich 1996). These results clearly demonstrate that pollinating bees are highly dependent on small-scale micro-habitats making them more susceptible to small-scale changes than to changes at the landscape level. Flower visitation rates of bees consistently decreased with increasing structural complexity of the landscape at the small as well as at the large spatial scale. Interestingly, higher visitation rates on trees located in structurally simple habitats and in landscapes with high proportions of unsuitable habitat did not affect fruit formation. Pollination success of wild cherries was not related to the visitation rates of bees indicating that even in structurally simple agricultural landscapes pollination success did not suffer and that pollinator visitation seemed not to limit seed set.

6.2 Seed dispersal

I investigated how seed dispersal of wild cherry seeds is affected by land-use intensification on small and large spatial scales (70 vs. 2,000 m). I aimed to assess the whole process of seed dispersal from seed removal by frugivorous seed dispersers up to the final seedling establishment after seed deposition. I used two different approaches to gain a comprehensive insight into the mechanism: 1) bird and mammal counts and tree observations at fruiting wild cherry trees and 2) VHF radio telemetry and feeding experiments to determine the movement behaviour of the main disperser species of the wild cherry, the Common Blackbird (*Turdus merula*, blackbirds hereafter).

First, I investigated how species richness, visitation rates and seed removal of wild cherry trees were affected by land-use intensification at two different spatial scales: at a local scale (vertical vegetation heterogeneity within a 70 m radius) and at a large spatial scale (landscape configuration in 2,000 m radius around focal trees). Species richness and total abundance of birds in the local community decreased with increasing land-use intensity, but unexpectedly this did not translate into decreased visitation rates or lower numbers of removed seeds at any of the observed spatial scales. For mammals, visitation rates even increased in structurally simpler landscapes at larger spatial scales. Thus, trees in structurally simple landscapes received as much disperser visits as trees in structurally complex landscapes, such as forests, and similar amounts of seeds were removed across all tree locations. Despite severely impoverished bird communities in structurally simple agricultural landscapes, birds found and visited wild cherry trees as often as in less degraded agricultural landscapes or forests. Attractive food sources like fruiting wild cherry trees (Snow and Snow 1988; Herrera 2002) might entice greater numbers of bird species and individuals to make long excursions to foraging trees (Herrera 2002). Another possible explanation would be adaptations in bird movement patterns by flying successively longer distances in structurally more simple landscapes; such adaptation could ultimately compensate for local land-use intensification (Sekercioglu et al. 2007).

To test the theory of adaptive movement behaviour for a single important disperser species, I investigated the movement patterns of blackbirds using VHF radio telemetry. Additionally, I performed feeding trials with wild blackbirds to calculate distributions of regurgitation times for wild cherry seeds. By combining the distributions of regurgitation times with the movement data in a simulation model, I was able to virtually track the movement of seeds through the landscape and to assess differences between different habitat types within the landscape matrix. Lastly, I used data on seedling recruitment for forest and farmland sites within the same landscape to investigate how the quality of seed dispersal was affected by land-use intensification. The simulations revealed that in structurally simple farmland habitats more cherry seeds were deposited directly under foraging trees compared to populations in forests. Median seed-dispersal distances as well as the proportion of long-distance dispersal events (distances > 100 m) were found to be lower in farmland than in forest populations. Blackbirds that inhabited forest habitats dispersed almost all seeds into suitable habitat whereas farmland blackbirds were significantly less efficient. Nevertheless, for both habitats, seed deposition in suitable habitat was much higher than would be expected from the proportion of suitable habitat within home ranges of the blackbirds. These findings indicate directed dispersal into suitable habitat by the dispersing blackbirds. The recorded seedling densities showed a much lower seedling establishment in farmland than forest populations. The survival probabilities of first-year seedlings showed the same trend and further supported the notion that shorter seed-dispersal distances in farmland than in forest habitats reduce seedling recruitment of wild cherries.

The combination of movement data from highly mobile seed dispersers such as blackbirds and the regurgitation times for swallowed seeds from feeding experiments provide reliable predictions for different aspects of seed-dispersal quality, such as seed-dispersal distances and the locations of seed deposition (Wang & Smith 2002; Schupp, Jordano & Gómez 2010).With the combination of the two approaches, I was able to assess all important stages within the life cycle of plant reproduction and to extend the knowledge about this process beyond the point of mere seed-dispersal quantity to seed-dispersal quality. My results demonstrate that blackbirds are highly efficient seed dispersers in temperate human-modified landscapes and that changes in their behaviour directly affect plant population dynamics. I conclude that tree populations in the farmland are more prone to extinction in the long term because of restricted seed exchange between populations and because of low levels of seedling recruitment. The findings clearly demonstrate that animal-mediated seed dispersal is an important ecosystem process, also in temperate ecosystems.

6.3 Synthesis

To understand the consequences of land-use change for plant reproduction and seed dispersal, it is necessary to study all involved ecosystem functions, i.e. pollination and seed dispersal. The complexity of ecosystem functions is illustrated by the variation in the responses of different contributing species to land-use change. Along the gradients of habitat structure and landscape configuration, i.e. at the small and the large spatial scale, visitation rates of bees, mammals and birds decreased, increased or remained constant, depending on the taxonomic group considered. While bees mainly reacted to small-scale changes of land-use, birds and mammals were affected at larger spatial scales. Thus, the shape of the curve relating ecosystem function to biodiversity is the sum of many individual curves from different taxonomic groups. Hence, the relationship found for one ecosystem function cannot necessarily be generalised to the same ecosystem function within another ecosystem or even to a completely different ecosystem function within the same landscape. Also, keystone species maintaining the ecosystem function may be more strongly affected by land-use intensification and on different scales than species that only play a marginal role for the respective function. These results highlight the importance of comprehensive studies that incorporate as much information of the contributing species as possible by using different methods and techniques. Studies that only look at specific aspects of an ecosystem function may lead to results that might not reflect the true response of an ecosystem function to land-use intensity.

In the wild cherry model system, neither pollination success, nor seed dispersal were finally influenced by land-use intensity at any of the spatial scales. This shows that changes in spatial movement patterns can buffer pollination and seed-dispersal interactions in highly mobile animal taxa, such as bees and birds. Thus, it is not only important to know how the landscape is configured, but also how the species that contribute to the respective ecosystem functions move through these landscapes. Highly mobile species might be able to move from one remaining semi-natural habitat structure to another, thereby stabilising the ecosystem function up to a certain degree of landscape degradation.

Overall, this study highlights that it is not sufficient to measure the species richness or the interaction frequency of pollinator or seed-disperser species to understand the ultimate consequences for the corresponding ecosystem function. Future studies quantifying the impacts of human disturbance on ecosystem functions should therefore also look at behavioural changes of pollinator and disperser species in response to human disturbance. In the cherry-blackbird system, a detailed analysis of the movement patterns of the most important seed disperser in forest and farmland habitats finally revealed a negative impact of land-use intensification on seedling recruitment of wild cherries although pollination and seed-removal rates were unaffected.

Thus, I found that plant populations in the farmland are more prone to extinction in the long term.

6.4 Future challenges

Future research should aim to study different ecosystem functions within the same landscape and cover the whole spectrum of species involved in maintaining the respective ecosystem functions. Such studies are needed for many different ecosystems in temperate as well as in subtropical and tropical regions, since results for one ecosystem function in a certain landscape cannot be transferred to different species communities or landscape characteristics. It is especially important to promote research of ecosystem functions in human-modified landscapes since these types of landscape will become more dominant in the future due to a growing human population. Thus, we urgently need information on how to create agricultural landscapes where the essential ecosystem processes such as pollination and seed dispersal can still be maintained by the contributing species. In the face of global climate change, such investigations also gain importance since plant species have to track their climatic niche, which in turn depends on the quality and quantity of seed dispersal and pollination services provided by animal vectors.

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10 Appendices

Appendix 1: Control variables – Materials and methods & Results

Methods

To account for potential differences in fruit availability and fruit traits among the study trees we determined for each tree crop size, general fruit availability in the neighbourhood, fruit size, fruit mass, fruit colour and genetic identity (Table A1.1).

Table A1.1: List of control variables.

Control variables
Crop size and fruit availability
Crop size
Tree and shrub species with fruits within 70 m
Total fruit abundance within 70 m
Fruit traits
Cherry diameter [mm]
Cherry weight [g]
Fruit colour [CIE L*a*b*]
L* (Luminosity)
a* (Indicator of magenta and green changes)
b* (Indicator of yellow and blue changes)
Genetic identity
Genetic identity

Crop size and fruit availability

We estimated crop size of each tree in the morning before starting the tree observations. If crop size was small all cherries in the crown were counted. For larger crop sizes, we counted cherries on representative branches and shoots of the tree crown and extrapolated to the whole crown. To record general fruit availability in the neighbourhood of the tree we recorded number of species, total number, and total crop sizes of fruiting trees and shrubs within a radius of 70 m around each study tree. Crop size and fruit availability were log(x + 1) transformed.

Fruit traits

To quantify fruit traits, we collected on average 48 cherries (range: 16–50) from each tree on the day of the tree observation, using pruning shears and a throwing bag sling. All fruits were weighted and the diameter at the point of the greatest diameter was measured. Fruit colour was assessed on the evening of the same day. We determined fruit colour of 10 fruits per tree with measurements taken from two opposite sides, using a spectrophotometer (SPECTRO 100, Instrument Systems GmbH, running IS-SPECTRA v. 3.73 software). We averaged the spectral curves over the two sides and the 10 fruits and translated them into CIE L*a*b* colour space. This colour system quantifies colour along three axes, luminosity (L*), an indicator of magenta and green changes (a*) and an indicator of yellow and blue changes (b*). For analysis we tested each of these axes separately.

Genetic identity

Genetic analyses of wild cherry trees were facilitated by recently established microsatellite markers (Schueler et al. 2003; Vaughan and Russell 2004). In the summer of 2006 we sampled a set of 23 wild cherry trees on various locations within the study area, of which eleven were later used as study trees (see Table A1.4, study trees in bold). For comparison with common cultivars, leaf material of eight different cultivars (Schneiders Späte Knorpelkirsche, Kordia, Regina, Hedelfinger Riesenkirsche, Sunburst, Sylvia, Sweetheart, Starking Hardy Giant) and three rootstocks (*Prunus avium* F12.1, Maxma 14, GieSelA 5) that are used for pomiculture within the study area was provided by the DLR Oppenheim from the experimental orchard in Ingelheim. Leaf material of another common garden form (*Prunus avium* L. ‘Plena’) was collected in the Botanical Gardens at the University of Mainz.

For DNA extraction we used a modification of the extraction protocol described in Wang et al. (1993). All leaves were dried over silica gel for at least 10 days. Then 10 to 15 mg of dry leaf tissue were grinded in a mixer mill (Retsch Mixer Mill MM 301, Retsch, Germany) for 3 minutes at 30 Hz using a 5 mm diameter stainless steel grinding ball (Retsch, Germany). After grinding, 40 µL 0.5 N NaOH for every mg leaf of tissue were added to the grinded leaf material. The tubes were then shaken shortly and centrifuged for 10 seconds up to 8000 rpm. From the supernatant, 5 µL were quickly transferred into a tube with 95 µL TRIS buffer pH 8.0.

PCRs were run on a TGradient Biometra Thermocycler (Biometra, Germany) using PCR beads (GE Healthcare PuReTaq™ Ready-To-Go™ PCR beads, GE Healthcare, UK). A 24 µL mixture of fluorescence labelled forward primer (Applied Biosystems, UK), unlabelled reverse primer (VBC-Biotech Service, Austria [Biozym Scientific, Germany]) and H_2O was added per tube. See Table A1.2 for detailed settings for each primer. We then added 1 µL of either the original extract (primer UDP96-001) or a further 1:5 dilution with TRIS buffer (all other primers).

A total of 4 µL of the PCR products (2 µL per primer, multiplex) per tube were transferred on a THERMOSPRINT® 96plate (BILATEC AG, Germany) and sealed with StarSeal Sealing Tape Polyolefin Film (STARLAB GmbH, Germany). Purification and gel run were performed by GENterprise (GENterprise GENOMICS, Gesellschaft für Genanalyse und Biotechnologie mbH, Mainz, Germany). During purification the 4 µL of the PCR products in each chamber of the plate were filled up to a volume of 10 µL adding Sephadex™ G-50 DNA Grade (GE Healthcare, UK) and H_2O. From these 10 µL, 4 µL per lane were used for a gel run on an ABI 3730 capillary sequencer (Applied Biosystems, CA, U.S.A.).

Table A1.2: PCR settings used for the seven SSR loci studied in *P. avium* L.

Locus code*	5'-Fluor Label	Dilution from original extract	Amount of primer used per sample [µL]	Annealing temperature [°C]	No. of Cycles
UDP96-001	FAM	1:1	0.4	50	34
UDP97-403	FAM	1:5	0.4	60	34
UDP98-412	NED	1:5	0.2	60	34
UDP98-410	FAM	1:5	0.4	60	34
UDP98-411	FAM	1:5	0.4	60	34
UDP98-021	NED	1:5	0.2	60	34
UDP96-005	NED	1:5	0.2	62	34

* Locus codes as in Cipriani et al. (1999), Testolin et al. (2000) and Schueler et al. (2003).

By comparing the SSR loci of wild cherry trees with that of the cultivars and rootstocks for all seven primers we tried to assign a set of 23 wild cherry trees sampled in 2006 to the cultivars. Tree individuals that could not be assigned to the cultivars were placed in the category “unknown” and might represent wild forms. Fragment lengths were analysed with ABI GeneMapper™ 3.5 software.

Statistical analysis of control variables

To assess the influence of the control variables (Table A1.1) on our results, we used simple linear regressions of all measures of tree visitors and seed removal against each control variable. If the relationship between, e.g. visitor species richness and a control variable was significant, we included that control variable as predictor variable in all analyses of visitor species richness. We then compared results from models with and without the control variable.

Results

Crop size and fruit availability

Crop size and general fruit availability in the neighbourhood of the trees had no significant influence on species richness nor on total number of tree visitors nor on fruit removal rate.

Fruit traits

Neither fruit colour nor cherry diameter or weight had any significant influence on species richness or on total number of tree visitors or on fruit removal rate.

Genetic Identity

With the exception of one tree that was identified as the cultivar “Schneiders Späte Knorpelkirsche”, microsatellite patterns for our study trees differed from all of the cultivars for which we had reference samples (Tables A1.4 and A1.5). Due to the distribution of trees that could be attributed to cultivars (*n* = 1) and not attributed to cultivars (*n* = 22), a rigorous statistical analysis of the effects of genetic identity on visitor assemblage and seed removal was not possible. The one identified cultivar was not visited by seed dispersers and had a seed removal rate of zero during our tree observations. Therefore, there is no indication that this tree attracted tree visitors disproportionately frequently or had an unusually high seed removal rate. The tree identified as cultivar was removed from the analyses, and trees with a similar growth form and fruit morphology were not sampled in the second year.

Table A1.4: Genetic identity of 23 cherry trees sampled in 2006 according to length of repeats at seven SSR loci. SSK = Schneiders Späte Knorpelkirsche; unknown = ancestry not known (tree could genetically not be identified as one of the sampled sweet cherry cultivars or rootstocks → Table A1.5). Numbers represent the allele sizes in base pairs. Trees also used for tree observations in the study printed in bold.

Study tree	UDP96-001	UDP97-403	UDP98-412	UDP98-410	UDP98-411	UDP98-021	UDP96-005	Identity
FF14	107/121	140/144	119/125	128/128	152/160	110/110	107/123	SSK
FF15	**103/121**	**128/128**	**119/123**	**128/130**	**164/166**	**100/114**	**103/123**	**unknown**
FF16B	107/123	142/144	119/125	128/128	152/160	110/114	121/123	unknown
FF17	107/115	122/140	119/119	130/132	152/152	100/110	97/103	unknown
FF26	123/123	118/118	119/119	122/128	164/176	100/100	97/107	unknown
FF27	121/123	unclear	119/119	130/130	164/164	100/100	107/115	unknown
FF31	121/121	120/140	111/119	128/130	140/170	100/114	107/123	unknown
FF32	123/123	118/138	117/119	128/130	166/176	100/100	103/123	unknown
FF33	123/123	118/118	117/119	130/130	164/164	100/102	103/123	unknown
FF34	121/123	unclear	117/119	128/130	160/164	100/110	103/123	unknown
FF35	**115/123**	**114/130**	**99/99**	**114/128**	**152/168**	**100/102**	**119/123**	**unknown**
FF40	**107/121**	**unclear**	**117/119**	**130/130**	**152/164**	**100/110**	**107/123**	**unknown**
FF42	**105/107**	**126/138**	**109/117**	**128/128**	**164/164**	**98/110**	**103/123**	**unknown**
FF43B	121/121	120/122	99/117	122/130	160/164	100/100	103/107	unknown
FF44	**107/101**	**140/144**	**119/119**	**122/122**	**164/164**	**102/114**	**103/115**	**unknown**
FF45	**123/123**	**122/140**	**119/119**	**128/132**	**160/162**	**100/100**	**103/115**	**unknown**
FF46	**107/121**	**122/140**	**99/119**	**122/128**	**164/164**	**100/100**	**123/123**	**unknown**
FF47	**121/121**	**122/140**	**119/123**	**128/136**	**160/164**	**110/110**	**107/123**	**unknown**
FW10	121/123	126/126	123/123	130/130	164/164	100/100	103/107	unknown
FW20	107/121	118/120	99/123	130/136	152/176	100/114	107/123	unknown
FW21	**121/121**	**122/138**	**119/123**	**130/130**	**164/166**	**114/114**	**107/123**	**unknown**
FW24	**121/121**	**120/122**	**117/119**	**122/128**	**160/164**	**102/110**	**107/127**	**unknown**
GW04	**148/148**	**122/124**	**99/117**	**128/128**	**160/176**	**100/100**	**107/123**	**unknown**

Table A1.5: Genotypes of nine sweet cherry cultivars and three sweet cherry rootstocks. Given are lengths of repeats at seven SSR loci. Numbers represent the allele sizes in base pairs.

Name	UDP96-001	UDP97-403	UDP98-412	UDP98-410	UDP98-411	UDP98-021	UDP96-005
Cultivars							
Schneiders Späte Knorpelkirsche	107/121	140/144	119/125	128/128	152/160	110/110	107/123
Kordia	107/121	142/144	119/125	128/128	152/160	110/110	107/123
Kordia*	107/121	142/144	117/119	128/128	152/160	110/110	107/123
Regina	107/121	140/144	119/119	122/128	152/166	100/110	103/123
Regina*	107/121	140/144	119/119	122/128	152/166	100/110	103/123
Hedelfinger Riesenkirsche	123/123	140/144	101/119	128/130	160/164	100/110	107/123
Sunburst	107/123	122/140	111/119	122/128	160/164	100/110	107/123
Sunburst*	107/123	122/140	111/119	122/128	160/164	100/110	107/123
Sylvia	107/123	122/138	109/117	122/128	160/164	100/110	107/123
Sweetheart	107/121	136/138	109/117	122/128	160/176	100/110	107/123
Starking Hardy Giant	107/123	122/140	119/119	122/128	152/160	100/110	107/123
Prunus avium L. 'Plena'	123/123	118/120	97/123	128/128	164/168	100/100	103/123
Rootstocks							
Prunus avium F12.1	121/123	144/144	117/123	128/136	152/164	100/100	115/123
Maxma 14	103/117	110/144	123/123	128/134	150/164	100/102	101/123
GieSelA 5	115/123	96/122	107/123	118/138	154/164	100/100	103/123

* Additional DNA samples obtained from Silvio Schueler and Alexandra Tusch for comparison of results (see Schueler et al. 2003).

To summarise, the control variables either did not influence tree visitors or including them in the statistical analyses did not change any of the results.

A1 References

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Appendix 2: Detailed results for the bird counts during the breeding season and the tree observations

To characterise the local bird community without the influence of fruiting wild cherry trees as attractive food resources we performed bird counts in spring before the ripening of the cherries. For the applied census methods see corresponding paragraph within the associated manuscript. The detailed results from the two spring bird censuses can be found below in Table A2.1.

The detailed results of the summer observations with all individual visits (including seed dispersers as well as all other visiting birds) can be found below in Table A2.2.

Table A2.1: Bird species observed in the neighbourhood of the 38 study trees during the breeding season in spring 2006 and 2007, ranked by total number of individuals at all tree locations and mean number of individuals per tree location.

Species*		Number of individuals	Mean no. of individuals per tree location
Common Starling	*Sturnus vulgaris*	201	5.29
Common Wood Pigeon	*Columba palumbus*	102	2.68
Common Chaffinch	*Fringilla coelebs*	76	2.00
Blue Tit	*Cyanistes caeruleus*	71	1.87
Common Blackbird	*Turdus merula*	66	1.74
Great Tit	*Parus major*	52	1.37
Eurasian Skylark	*Alauda arvensis*	46	1.21
Carrion Crow	*Corvus corone*	38	1.00
Yellowhammer	*Emberiza citrinella*	34	0.89
Eurasian Blackcap	*Sylvia atricapilla*	34	0.89
European Robin	*Erithacus rubecula*	28	0.74
European Goldfinch	*Carduelis carduelis*	27	0.71
Common Chiffchaff	*Phylloscopus collybita*	25	0.66
Eurasian Jay	*Garrulus glandarius*	23	0.61
Eurasian Magpie	*Pica pica*	17	0.45
Barn Swallow	*Hirundo rustica*	16	0.42
Common Pheasant	*Phasianus colchicus*	15	0.39
Common Kestrel	*Falco tinnunculus*	14	0.37
Common Buzzard	*Buteo buteo*	13	0.34
Great Spotted Woodpecker	*Dendrocopos major*	13	0.34
Firecrest	*Regulus ignicapilla*	13	0.34
Garden Warbler	*Sylvia borin*	13	0.34
Winter Wren	*Troglodytes troglodytes*	13	0.34
Common Whitethroat	*Sylvia communis*	12	0.32

Table A2.1 continued.

Species*		Number of individuals	Mean no. of individuals per tree location
Fieldfare	*Turdus pilaris*	11	0.29
Long-tailed Bushtit	*Aegithalos caudatus*	10	0.26
Mistle Thrush	*Turdus viscivorus*	10	0.26
European Greenfinch	*Carduelis chloris*	9	0.24
Black Redstart	*Phoenicurus ochruros*	9	0.24
Common Nightingale	*Luscinia megarhynchos*	8	0.21
Eurasian Tree Sparrow	*Passer montanus*	8	0.21
Western Jackdaw	*Corvus monedula*	7	0.18
White Wagtail	*Motacilla alba*	7	0.18
Common Linnet	*Carduelis cannabina*	6	0.16
European Turtle Dove	*Streptopelia turtur*	6	0.16
Short-toed Treecreeper	*Certhia brachydactyla*	5	0.13
Corn Bunting	*Emberiza calandra*	5	0.13
Willow Warbler	*Phylloscopus trochilus*	5	0.13
Eurasian Nuthatch	*Sitta europaea*	5	0.13
Grey Partridge	*Perdix perdix*	*4*	*0.11*
Coal Tit	*Periparus ater*	4	0.11
Eurasian Stonechat	*Saxicola torquatus*	4	0.11
European Serin	*Serinus serinus*	4	0.11
Eurasian Golden Oriole	*Oriolus oriolus*	3	0.08
European Green Woodpecker	*Picus viridis*	3	0.08
Dunnock	*Prunella modularis*	3	0.08
Eurasian Bullfinch	*Pyrrhula pyrrhula*	3	0.08
Song Thrush	*Turdus philomelos*	3	0.08
Common Swift	*Apus apus*	2	0.05
Grey Heron	*Ardea cinerea*	2	0.05
Eurasian Treecreeper	*Certhia familiaris*	2	0.05
Western Marsh Harrier	*Circus aeruginosus*	2	0.05
Hawfinch	*Coccothraustes coccothraustes*	2	0.05
Wood Warbler	*Phylloscopus sibilatrix*	2	0.05
Marsh Tit	*Poecile palustris*	2	0.05
Goldcrest	*Regulus regulus*	2	0.05
Eurasian Collared Dove	*Streptopelia decaocto*	2	0.05
Montagu's Harrier	*Circus pygargus*	1	0.03
Common Pigeon	*Columba livia* [*domestica*]	1	0.03
Rook	*Corvus frugilegus*	1	0.03
European Pied Flycatcher	*Ficedula hypoleuca*	1	0.03
Black Kite	*Milvus migrans*	1	0.03
Western Yellow Wagtail	*Motacilla flava*	1	0.03
House Sparrow	*Passer domesticus*	1	0.03
Willow Tit	*Poecile montana*	1	0.03
Lesser Whitethroat	*Sylvia curruca*	1	0.03

* Bird taxonomy followed the recommendations of the International Ornithological Congress (see Gill and Wright 2006).

Table A2.2: Bird species observed as visitors of 38 wild cherry trees in 2006 and 2007, ranked by total number of visits at all trees and mean number of visits per tree.

Species[*]		**Number of individuals**	**Mean no. of individuals per tree location**
Common Starling[†]	*Sturnus vulgaris*	434	11.42
Common Blackbird[†]	*Turdus merula*	398	10.47
Eurasian Blackcap[†]	*Sylvia atricapilla*	274	7.21
Blue Tit	*Cyanistes caeruleus*	238	6.26
Great Tit[†]	*Parus major*	189	4.97
Garden Warbler[†]	*Sylvia borin*	96	2.53
Common Chaffinch[†]	*Fringilla coelebs*	73	1.92
Yellowhammer	*Emberiza citrinella*	67	1.76
Great Spotted Woodpecker[†]	*Dendrocopos major*	59	1.55
Common Wood Pigeon[†]	*Columba palumbus*	42	1.11
Common Whitethroat[†]	*Sylvia communis*	42	1.11
Song Thrush[†]	*Turdus philomelos*	42	1.11
Eurasian Jay[†]	*Garrulus glandarius*	36	0.95
Hawfinch[†]	*Coccothraustes coccothraustes*	35	0.92
Mistle Thrush[†]	*Turdus viscivorus*	27	0.71
Eurasian Magpie	*Pica pica*	24	0.63
Eurasian Golden Oriole[†]	*Oriolus oriolus*	21	0.55
Carrion Crow[†]	*Corvus corone*	20	0.53
Eurasian Nuthatch[†]	*Sitta europaea*	20	0.53
Fieldfare[†]	*Turdus pilaris*	19	0.50
House Sparrow	*Passer domesticus*	16	0.42
Common Chiffchaff	*Phylloscopus collybita*	14	0.37
Willow Warbler	*Phylloscopus trochilus*	12	0.32
Long-tailed Bushtit	*Aegithalos caudatus*	11	0.29
Marsh Tit	*Poecile palustris*	11	0.29
Common Kestrel	*Falco tinnunculus*	9	0.24
Tree Pipit	*Anthus trivialis*	8	0.21
Eurasian Stonechat	*Saxicola torquatus*	8	0.21
Black Redstart	*Phoenicurus ochruros*	6	0.16
Eurasian Skylark	*Alauda arvensis*	4	0.11
Red-backed Shrike	*Lanius collurio*	4	0.11
Coal Tit	*Periparus ater*	4	0.11
European Serin	*Serinus serinus*	4	0.11
European Turtle Dove	*Streptopelia turtur*	4	0.11
Common Buzzard	*Buteo buteo*	3	0.08
European Goldfinch	*Carduelis carduelis*	3	0.08
European Pied Flycatcher	*Ficedula hypoleuca*	3	0.08
Common Linnet	*Carduelis cannabina*	2	0.05
European Greenfinch	*Carduelis chloris*	2	0.05
Corn Bunting	*Emberiza calandra*	2	0.05
European Green Woodpecker	*Picus viridis*	2	0.05
Eurasian Bullfinch	*Pyrrhula pyrrhula*	2	0.05
Little Owl	*Athene noctua*	1	0.03
Great Grey Shrike	*Lanius excubitor*	1	0.03
White Wagtail	*Motacilla alba*	1	0.03
Western Yellow Wagtail	*Motacilla flava*	1	0.03
Spotted Flycatcher	*Muscicapa striata*	1	0.03
Common Pheasant	*Phasianus colchicus*	1	0.03
Dunnock	*Prunella modularis*	1	0.03
Whinchat	*Saxicola rubetra*	1	0.03

[†] Seed dispersers of the wild cherry.

A2 References

Gill F and Wright M on behalf of the International Ornithological Congress (2006): Birds of the World: Recommended English Names. Princeton University Press, Princeton, USA.

Appendix 3: Categorisation of suitable habitat from CORINE 2006 data of land-use

Table A3.1: Suitable habitat types in the study (CLC codes and classes with average proportion in 2,000 m radius over all study trees; *n.a.* if no such habitat occurred in any of the 2,000 m radii) that had been classified for the different functional groups of ecosystem service providers. For the mammals habitat types were separated into suitable habitat (extensively used farmland) and forest.

CLC code	CLC class	Average proportion in 2,000 m radius [%]
Bees (semi-natural habitat types)		
242	Complex cultivation patterns	5.3
243	Land principally occupied by agriculture, with significant areas of natural vegetation	1.6
231	Pastures	0.3
321	Natural grasslands	0.2
324	Transitional woodland-shrub	0.1
Birds (semi-natural habitat types)		
311	Broadleaved forest	11.1
313	Mixed forest	3.5
312	Coniferous forest	2.1
324	Transitional woodland shrub	0.6
321	Natural grasslands	0.1
322	Moors and heathland	*n.a.*
Mammals (suitable habitat types)		
Extensively used farmland		
242	Complex cultivation patterns	7.6
231	Pastures	2.4
243	Land principally occupied by agriculture, with significant areas of natural vegetation	1.8
324	Transitional woodland shrub	0.3
321	Natural grassland	*n.a.*
322	Moors and heathland	*n.a.*
Forest		
311	Broadleaved forest	16.5
313	Mixed forest	4.0
312	Coniferous forest	0.3

Appendix 4: Statistical summary of linear regressions and SARs

Table 4.1: Summary statistics for all analyses. Moran's I values are given for the residuals of the linear regressions (LMs = linear regression models) together with an indicator of *significance level* from simple regression analyses: *** = $P \leq 0.001$; ** = $P \leq 0.01$; * = $P \leq 0.05$. Spatial autoregressive models (SARs) were calculated for LMs with significant autocorrelation. Resulting Moran's I values are given for the residuals of the SARs, again together with an indicator of *significance level* (see above).

		LMs				**SAR**		
	n	*r*	*t*	*P*	*Moran's I*	*z*	*P*	*Moran's I*
Species richness in the local community								
Bees	32							
verticalVH (70 m)		–0.43	–2.64	0.013	**0.27** **	–3.04	0.002	< –0.001
% semi-natural habitat < 2,000 m		–0.03	–0.15	0.882	**0.21** *	-0.06	0.952	< –0.001
Birds[1]	38							
verticalVH (70 m)		0.81	8.22	< 0.001	–0.08			
% semi-natural habitat < 2,000 m		0.38	2.45	0.019	0.05			
Tree vistation rates								
Bees	32							
verticalVH (70 m)		–0.37	–2.19	0.037	0.09			
% semi-natural habitat < 2,000 m		–0.46	–2.15	0.039	0.06			
Birds[1]	38							
verticalVH (70 m)		0.08	0.51	0.612	–0.02			
% semi-natural habitat < 2,000 m		0.15	0.90	0.373	–0.01			
Mammals	21							
verticalVH (70 m)		0.07	0.30	0.767	**0.37** ***	–0.22	0.826	–0.03
% extensively used farmland < 2,000 m		0.50	2.53	0.020	–0.02			
% forest < 2,000		0.29	1.34	0.196	**0.35** ***	0.34	0.257	–0.03
Ecosystem function								
Pollination success	32							
verticalVH (70 m)		–0.06	–0.34	0.736	–0.11			
% semi-natural habitat < 2,000 m		–0.14	–0.75	0.461	–0.13			
Seed removal by birds	38							
verticalVH (70 m)		< 0.01	0.04	0.966	0.04			
% semi-natural habitat < 2,000 m		0.15	0.88	0.384	0.03			

[1] disperser species

Appendix 5: Results of trapping

Table 5.1: List of bee species that had been recovered from all pan traps used in the study. The honeybee appears first in the table, then the wild bee species, followed by the bumblebee species.

Species[1]	**Individuals**
Apis *mellifera* Linnaeus, 1758	15
Andrena *bicolor* Fabricius, 1775	26
Andrena chrysosceles (Kirby, 1802)	2
Andrena cineraria (Linnaeus, 1758)	11
Andrena distinguenda Schenck 1871	1
Andrena dorsata (Kirby 1802)	56
Andrena eximia Smith, 1847	1
Andrena flavipes Panzer, 1799	120
Andrena fucata Smith, 1847	1
Andrena fulva (Müller, 1766)	26
Andrena fulvata E. Stöckhert, 1930	11
Andrena gravida Imhoff, 1832	2
Andrena haemorrhoa (Fabricius, 1781)	68
Andrena helvola (Linnaeus, 1758)	7
Andrena jacobi Perkins, 1921	14
Andrena labiata Fabricius, 1781	1
Andrena lagopus Latreille, 1809	21
Andrena minutula (Kirby, 1802)	71
Andrena nigroaena (Kirby, 1802)	3
Andrena nitida (Müller, 1776)	14
Andrena pilipes Fabricius, 1781	1
Andrena praecox (Scopoli, 1763)	5
Andrena propinqua (Schenck, 1853)	1
Andrena subopaca Nylander, 1848	26
Andrena synadelpha Perkins, 1914	1
Andrena tibialis (Kirby, 1802)	4
Andrena varians (Rossi, 1792)	2
Andrena ventralis Imhoff, 1832	2
Anthophora *plumipes* Pallas, 1772	1
Ceratina *chalcites* Germar, 1839	5
Ceratina cucurbitina (Rossi, 1792)	4
Colletes *cunicularius* (Linnaeus, 1761)	11
Halictus *scabiosae* (Rossi, 1790)	1
Halictus tumulorum (Linnaeus, 1758)	2
Lasioglossum *calceatum* (Scopoli, 1763)	39
Lasioglossum glabriusculum (Morawitz, 1872)	3
Lasioglossum laticeps (Schenck, 1868)	14

Table 5.1 continued

Species[1]	**Individuals**
Lasioglossum lineare (SCHENCK, 1868)	96
Lasioglossum malachurum (KIRBY, 1802)	384
Lasioglossum minutissimum (KIRBY, 1802)	6
Lasioglossum minutulum (SCHENCK, 1853)	1
Lasioglossum morio (FABRICIUS, 1793)	32
Lasioglossum parvulum (SCHENCK, 1853)	1
Lasioglossum pauperatum (BRULLÉ, 1832)	5
Lasioglossum pauxillum (SCHENCK, 1853)	37
Lasioglossum politum (SCHENCK, 1853)	1
Lasioglossum punctatissimum (SCHENCK, 1853)	2
Lasioglossum puncticolle (MORAWITZ, 1872)	2
Lasioglossum pygmaeum (SCHENCK, 1853)	4
Lasioglossum subhirtum (LEPELETIER, 1841)	6
Lasioglossum xanthopus (KIRBY, 1802)	10
Nomada *alboguttata* HERRICH-SCHÄFFER, 1839	1
Nomada bifasciata OLIVIER, 1811	1
Nomada castellana DUSMET, 1913	1
Nomada fabriciana (LINNAEUS, 1767)	6
Nomada facilis SCHWARZ, 1967	1
Nomada ferruginata (LINNAEUS, 1767)	1
Nomada flava PANZER, 1798	4
Nomada flavoguttata (KIRBY, 1802)	46
Nomada lathburiana (KIRBY, 1802)	1
Nomada marshamella (KIRBY, 1802)	1
Nomada ruficornis (LINNAEUS, 1758)	1
Nomada sheppardana (KIRBY, 1802)	7
Nomada signata JURINE, 1807	1
Nomada zonata PANZER, 1798	1
Osmia *aurulenta* (PANZER, 1799)	1
Osmia bicolor (SCHRANK, 1781)	4
Osmia bicornis (LINNAEUS, 1758) [syn. *Osmia rufa* (LINNAEUS, 1758)]	12
Osmia cornuta (LATREILLE, 1805)	2
Osmia gallarum SPINOLA, 1808	2
Sphecodes *ephpippius* (LINNAEUS, 1767)	1
Sphecodes longulus VON HAGENS, 1882	4
Sphecodes majalis PÉREZ, 1903	1
Sphecodes monilicornis (KIRBY, 1802)	1
Sphecodes niger VON HAGENS, 1874	3
Bombus *lapidarius* (LINNAEUS, 1758)	2
Bombus pascuorum (SCOPOLI, 1763)	2
Bombus pratorum (LINNAEUS, 1761)	3
Bombus terrestris (LINNAEUS, 1758)	8

Table 5.1 continued

Species[1]	**Individuals**
***Psithyrus** bohemicus* (SEIDEL, 1837)	2
Psithyrus sylvestris (LEPELETIER, 1832)	1
Psithyrus vestalis (GEOFFROY, 1785)	2

[1] Species classification after Scheuchl (2000, 2006) and Schmid-Egger & Scheuchl (1997) and occasionally after Armiet (1999), Armiet et al. (1999, 2001, 2004, 2007).

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Appendix 6: Statistical summary of AICc calculations from multiple regressions

Table 6.1 Effects of vertical vegetation heterogeneity (*verticalVH*) at the small spatial scale and of the proportion of suitable habitat at 2,000 m radius on species richness, visitation rates of bees and mean seed set of cherry trees. AICc and ΔAICc values as well as Akaike weights were calculated for four linear models for each response variable. Best models are printed in *bold*.

Predictor	***n***	*AICc*	*ΔAICc*	*Akaike weight*
Species richness in the local community	32			
~ verticalVH + %seminat2000m		191.897	2.074	0.235
~ verticalVH		**198.823**	**0.000**	**0.662**
~ %seminat2000m		196.489	6.666	0.024
~ 1		194.070	4.247	0.079
Tree vistation rates	32			
~ verticalVH + %seminat2000m		**3.837**	**0.000**	**0.309**
~ verticalVH		**3.850**	**0.013**	**0.307**
~ %seminat2000m		**3.990**	**0.152**	**0.287**
~ 1		6.149	2.312	0.097
Ecosystem function/Pollination success	32			
~ verticalVH + %seminat2000m		–31.189	4.473	0.059
~ verticalVH		–33.341	2.320	0.173
~ %seminat2000m		–33.808	1.853	0.218
~ 1		**–35.661**	**0.000**	**0.551**

Appendix 7: Distribution of regurgitation times (RTs)

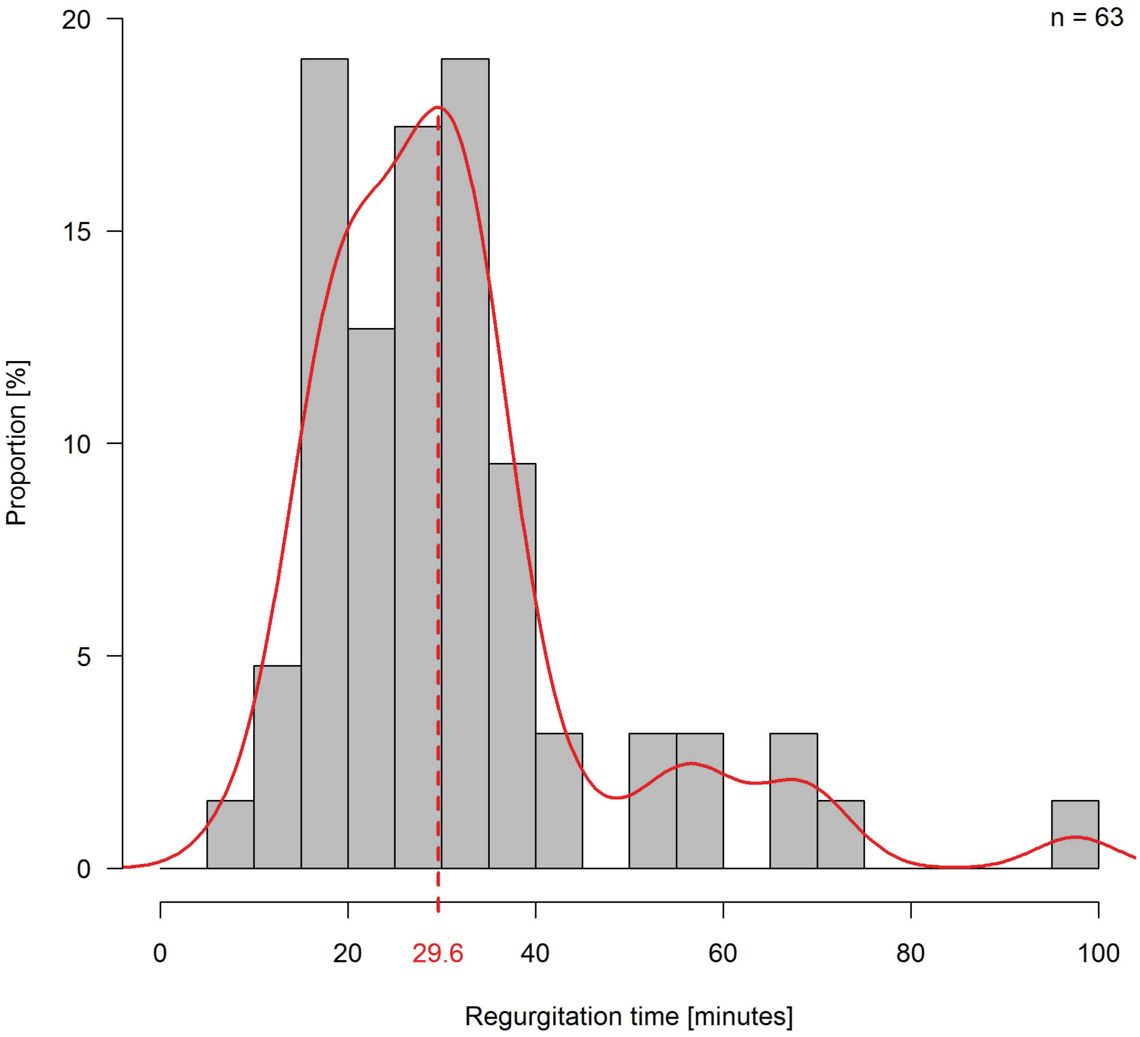


Figure A7.1: Distribution of regurgitation times from 63 feeding trials with 15 adult male Common Blackbirds (*Turdus merula* L.). RT values ranged from 8 to 98 minutes and are shown in 5-minute steps (*grey bars*); the red curve represents the fitted density distribution with a smoothing factor of 5 minutes; median RT is indicated by the *dashed red line*.

Table A7.1: Distribution of proportions (percentages) for each time interval according to the fitted RT distribution (see Fig. A7.1 above).

Time interval [min]	Poportion [%]	Number of cases out of 10,000 samples
8	0.56	56
9	0.71	71
10	0.89	89
11	1.09	109
12	1.31	131
13	1.55	155
14	1.80	180
15	2.05	205
16	2.29	229
17	2.50	250
18	2.70	270
19	2.86	286
20	2.99	300
21	3.10	310
22	3.19	319
23	3.27	327
24	3.34	334
25	3.40	340
26	3.46	346
27	3.51	352
28	3.54	354
29	3.55	355
30	3.52	352
31	3.45	345
32	3.34	334
33	3.18	318
34	2.98	298
35	2.74	274
36	2.47	247
37	2.19	219
38	1.91	191
39	1.64	165
40	1.38	138
41	1.15	115
42	0.96	96
43	0.79	79
44	0.66	66
45	0.55	55

Table A7.1: continued.

Time interval [min]	Poportion [%]	Number of cases out of 10,000 samples
46	0.48	48
47	0.43	43
48	0.40	40
49	0.38	38
50	0.38	38
51	0.39	39
52	0.41	41
53	0.43	43
54	0.45	45
55	0.47	47
56	0.48	48
57	0.48	48
58	0.47	47
59	0.47	47
60	0.45	45
61	0.44	44
62	0.43	43
63	0.43	43
64	0.42	42
65	0.42	42
66	0.41	41
67	0.41	41
68	0.40	40
69	0.38	38
70	0.36	36
71	0.33	33
72	0.30	30
73	0.26	26
74	0.22	22
75	0.18	18
76	0.14	14
77	0.11	11
78	0.08	8
79	0.06	6
80	0.04	4
81	0.03	3
82	0.02	2
83	0.01	1
84	0.01	1

Table A7.1 continued.

Time interval [min]	Poportion [%]	Number of cases out of 10,000 samples
85	0.01	1
86	0.01	1
87	0.02	2
88	0.02	2
89	0.03	3
90	0.04	4
91	0.06	6
92	0.07	7
93	0.09	9
94	0.10	10
95	0.11	11
96	0.12	12
97	0.13	13
98	0.13	13

Appendix 8: Categorisation of suitable habitat from ATKIS DLM data of land-use

Table A8.1: Habitat types within the study area (ATKIS attributes and object codes) that had been classified as suitable for the wild cherry (*P. avium*).

ATKIS attribute	ATKIS object code
4102_2740	Roadside green belts
4102_9998	Grassland (fallow land and shrubland)
4102_9999	Grassland (transitional woodland)
4104_0000	Heath
4107_1000	Forest, cultivated forest (broad-leafed forest)
4107_3000	Forest, cultivated forest (mixed forest)
4108_1000	Small woods, cultivated forest (broad-leafed forest)
4108_3000	Small woods, cultivated forest (mixed forest)
4202_0000	Row of trees, alley
4203_0000	Hedge, hedge-bank

Table A8.2: Habitat types within the study area (ATKIS attributes and object codes) that had been classified as forest or farmland.

ATKIS attribute	ATKIS object code
Forest	
4107_1000	Forest, cultivated forest (broad-leafed forest)
4107_3000	Forest, cultivated forest (mixed forest)
Farmland	
4102_2740	Roadside green belts
4102_9998	Grassland (fallow land and shrubland)
4102_9999	Grassland (transitional woodland)
4104_0000	Heath
4108_1000	Small woods, cultivated forest (broad-leafed forest)
4108_3000	Small woods, cultivated forest (mixed forest)
4202_0000	Row of trees, alley
4203_0000	Hedge, hedge-bank

Appendix 9: Individual-based seed-dispersal distances

The following pages show the individual seed-dispersal distributions (SDDs) of 32 Common Blackbirds (*Turdus merula* L.).

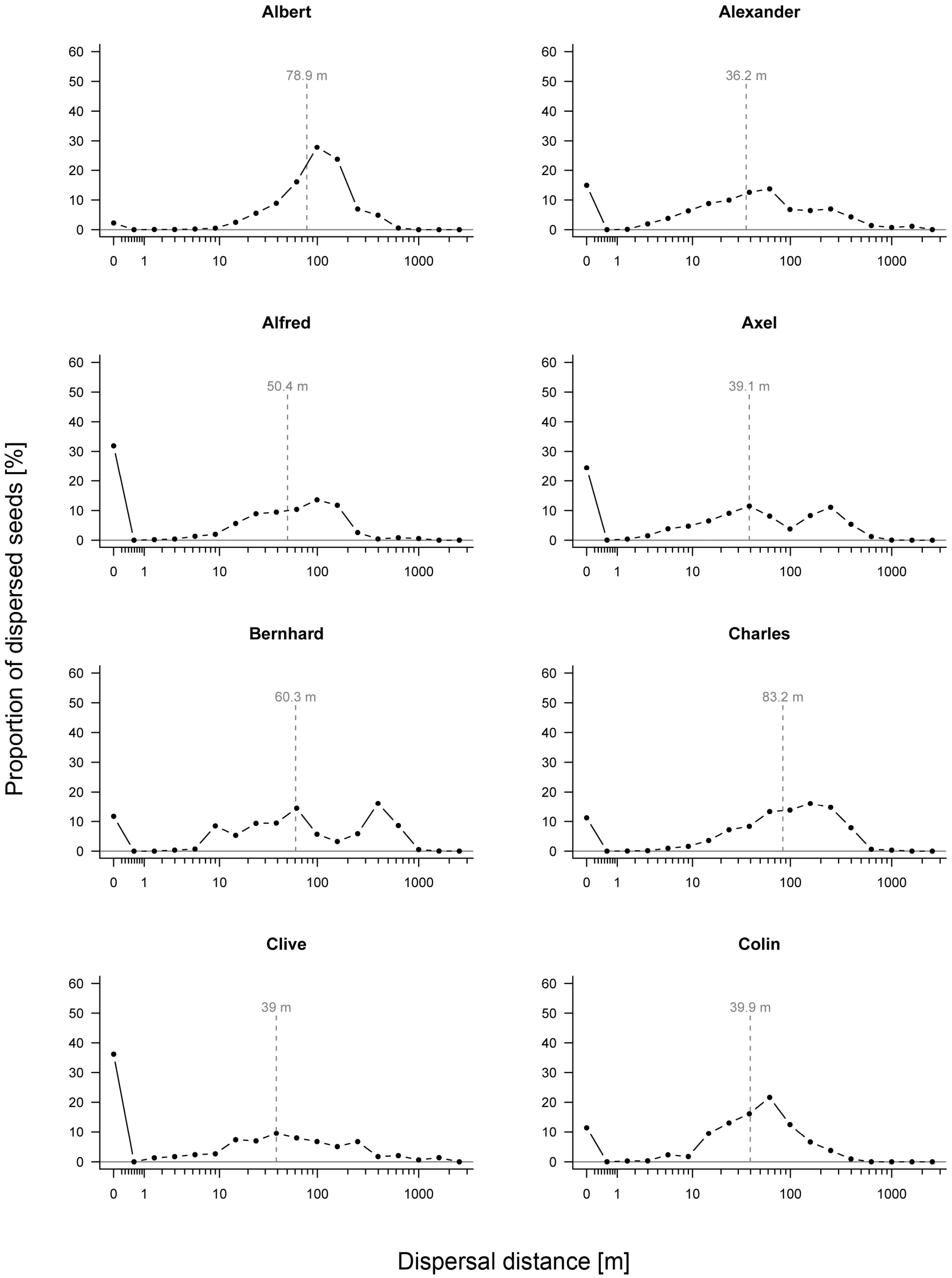


Figure A9.1: Seed-dispersal distributions of 32 Common Blackbirds; median seed-dispersal distance is indicated by a *dashed line*.

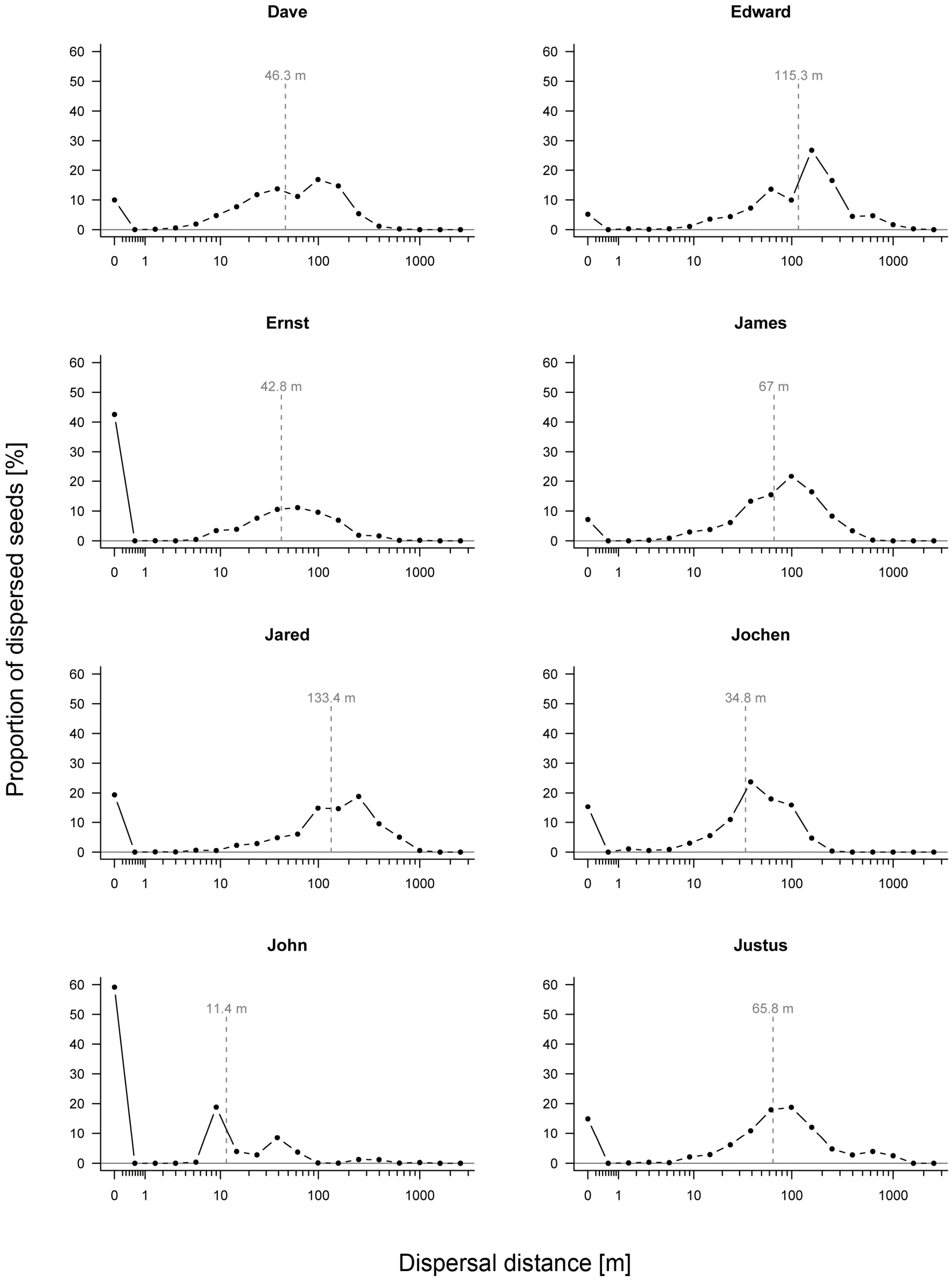


Figure A9.1 continued.

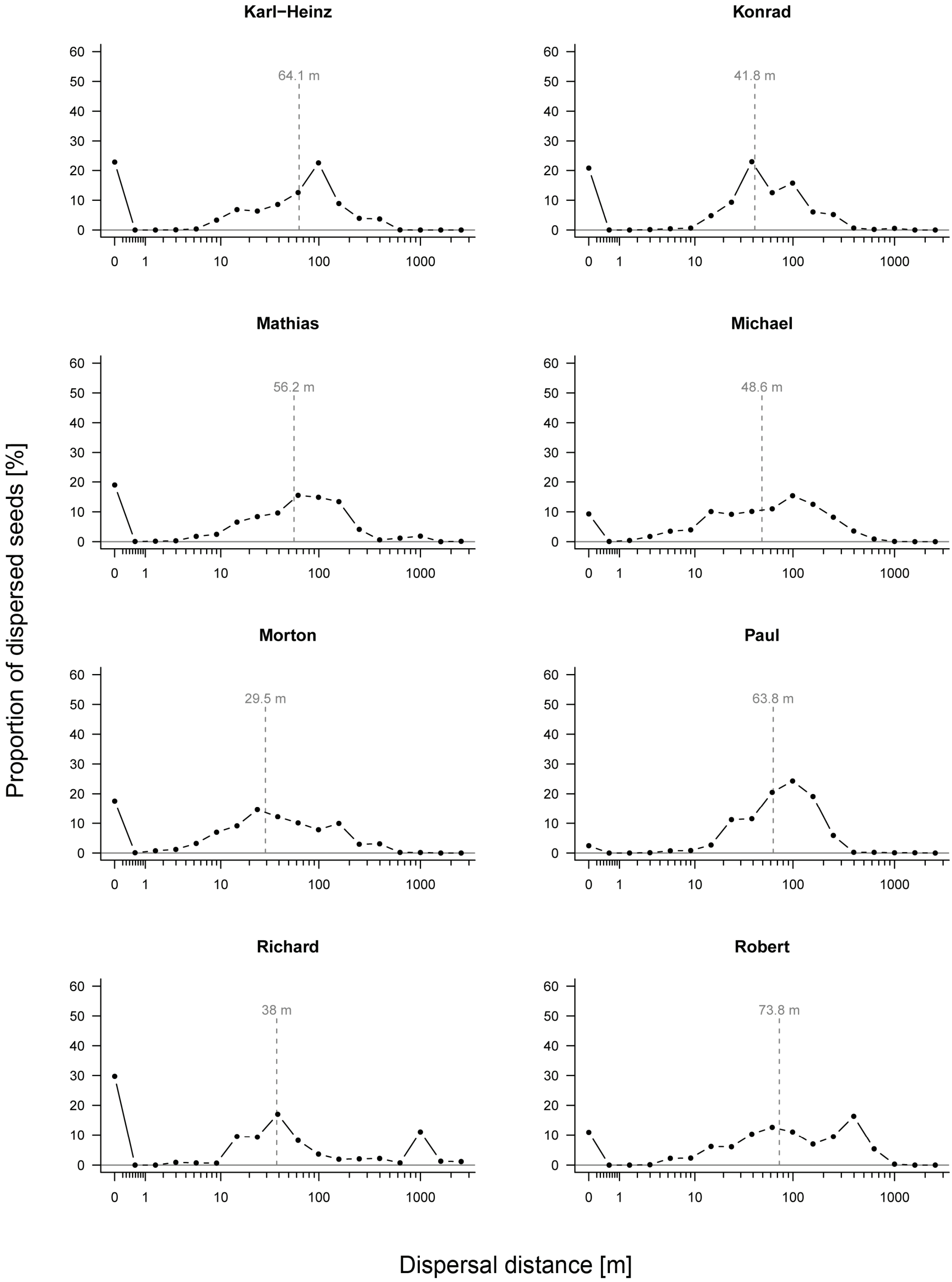
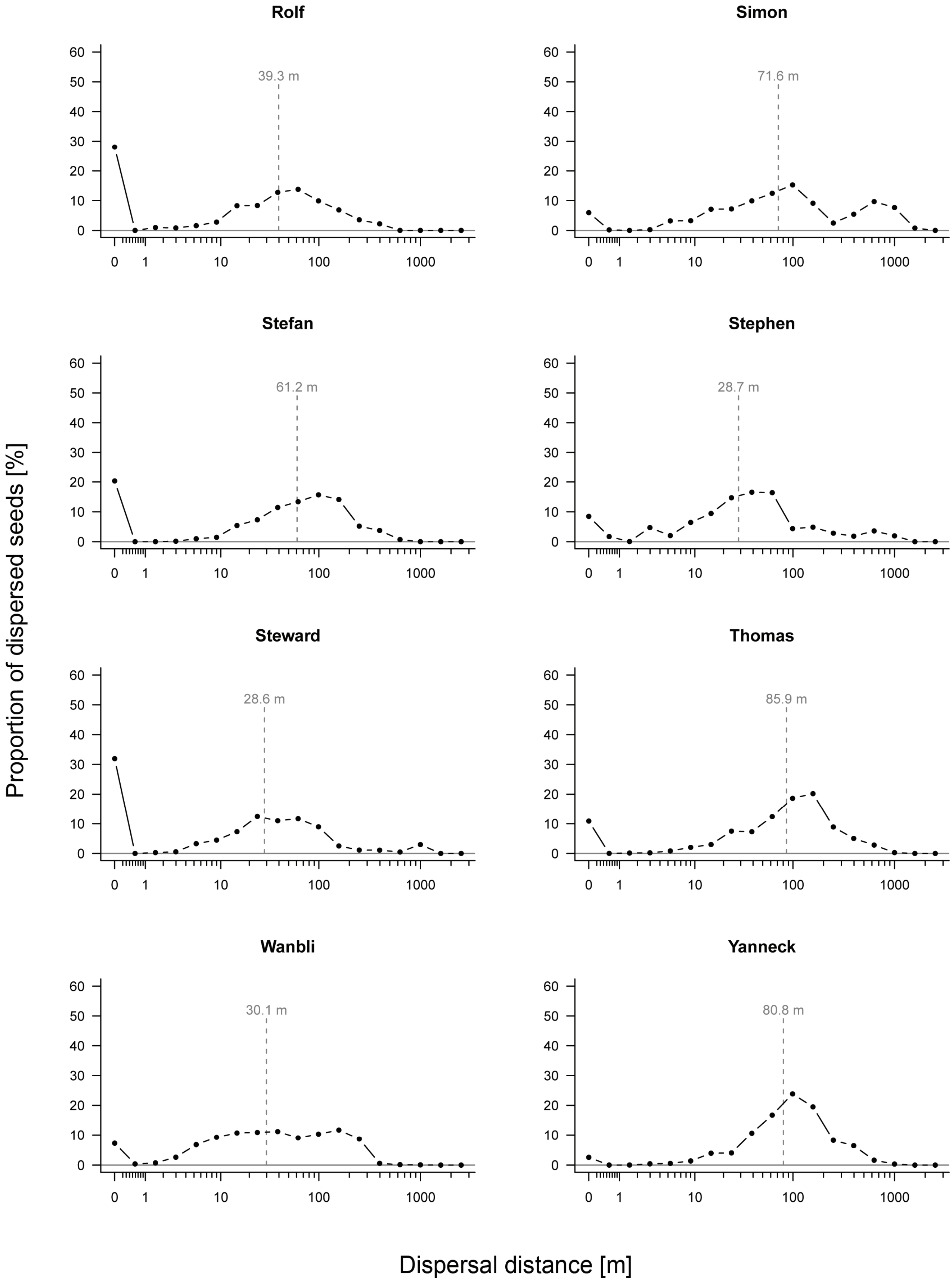


Figure A9.1 continued.


Rolf
39.3 m
Simon
71.6 m
Stefan
61.2 m
Stephen
28.7 m
Steward
28.6 m
Thomas
85.9 m
Wanbli
30.1 m
Yanneck
80.8 m
0
10
20
30
40
50
60
0
1
10
100
1000
Proportion of dispersed seeds [%]
Dispersal distance [m]

Appendix 10: Individual-based habitat-specific seed-dispersal distances for 30 Common Blackbirds

The following pages show the individual seed-dispersal distributions (SDDs) of 30 Common Blackbirds (*Turdus merula* L.) separated according to habitat type. Figure A10.1 shows the results for 9 forest individuals and Figure A10.2 for 21 farmland individuals.

The distributions of each habitat category were further split into seeds that were deposited either into suitable habitats for the wild cherry (*green curve*) or into unsuitable habitats (*red curve*) after dispersal by the birds. For each curve the median of the SDD is indicated (*dashed line*) and the corresponding value is given in meters.

Two barplots are included in each graph to illustrate the differences between the distributions of present suitable habitat (*pres. SH*) calculated from the habitat area inside the individual home range and predicted seed dispersal (*pred. SD*) calculated from the individual movement data. The amount of suitable habitat is plotted in *green* while the amount of unsuitable habitat is plotted in *red*.

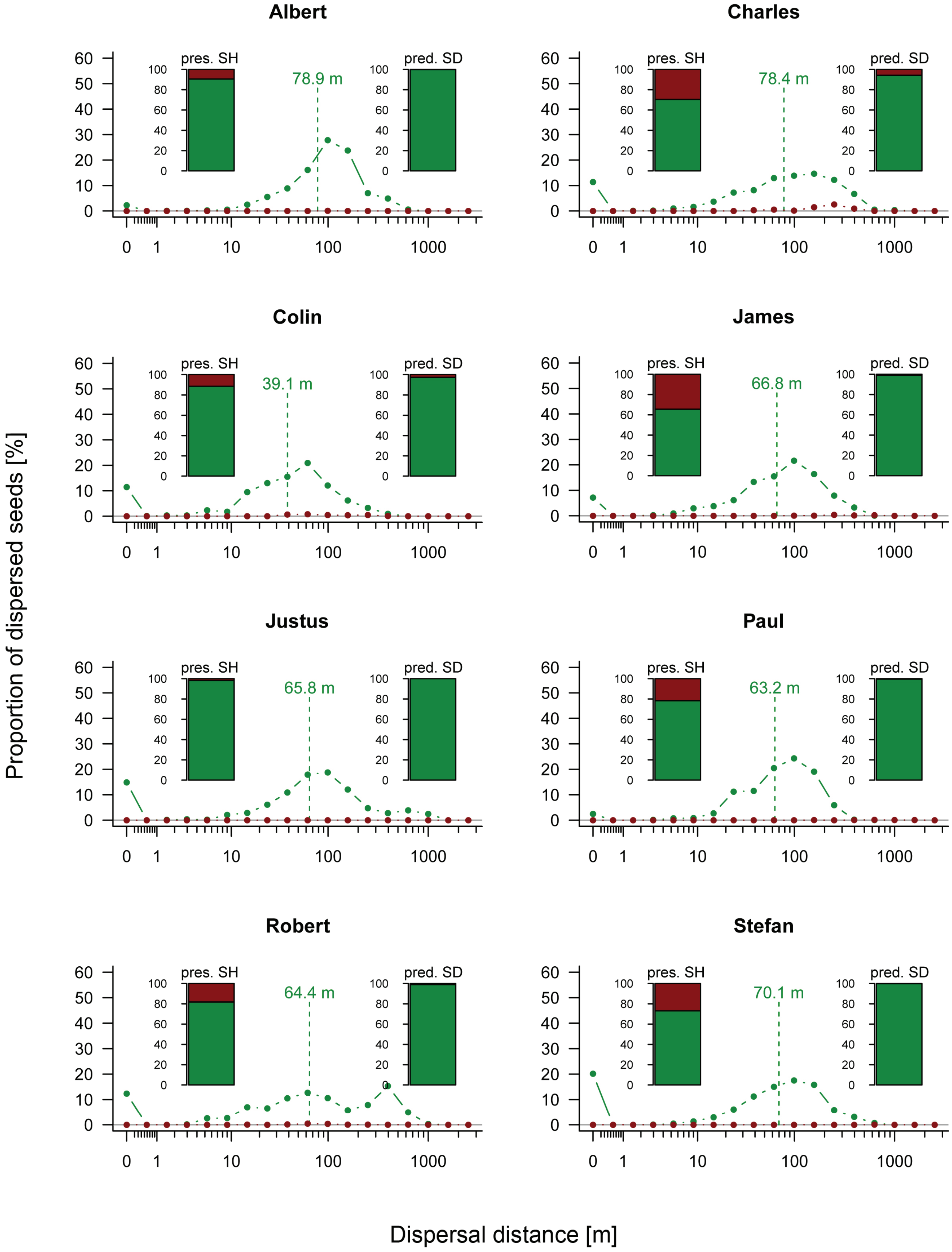


Figure A10.1: Individual-based seed-dispersal into suitable (*green*) and unsuitable (*red*) habitat for 9 forest-dwelling Common Blackbirds with the median seed dispersal distance (*dashed line*). Bars indicate the proportions of present suitable habitat (*pres. SH*) inside the home range of each bird and the predicted seed dispersal (*pred. SD*) from the models into either suitable (*green*) or unsuitable habitat (*red*).

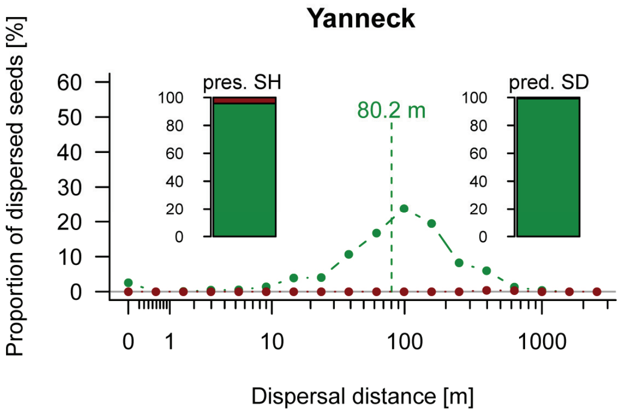


Figure A10.1 continued.

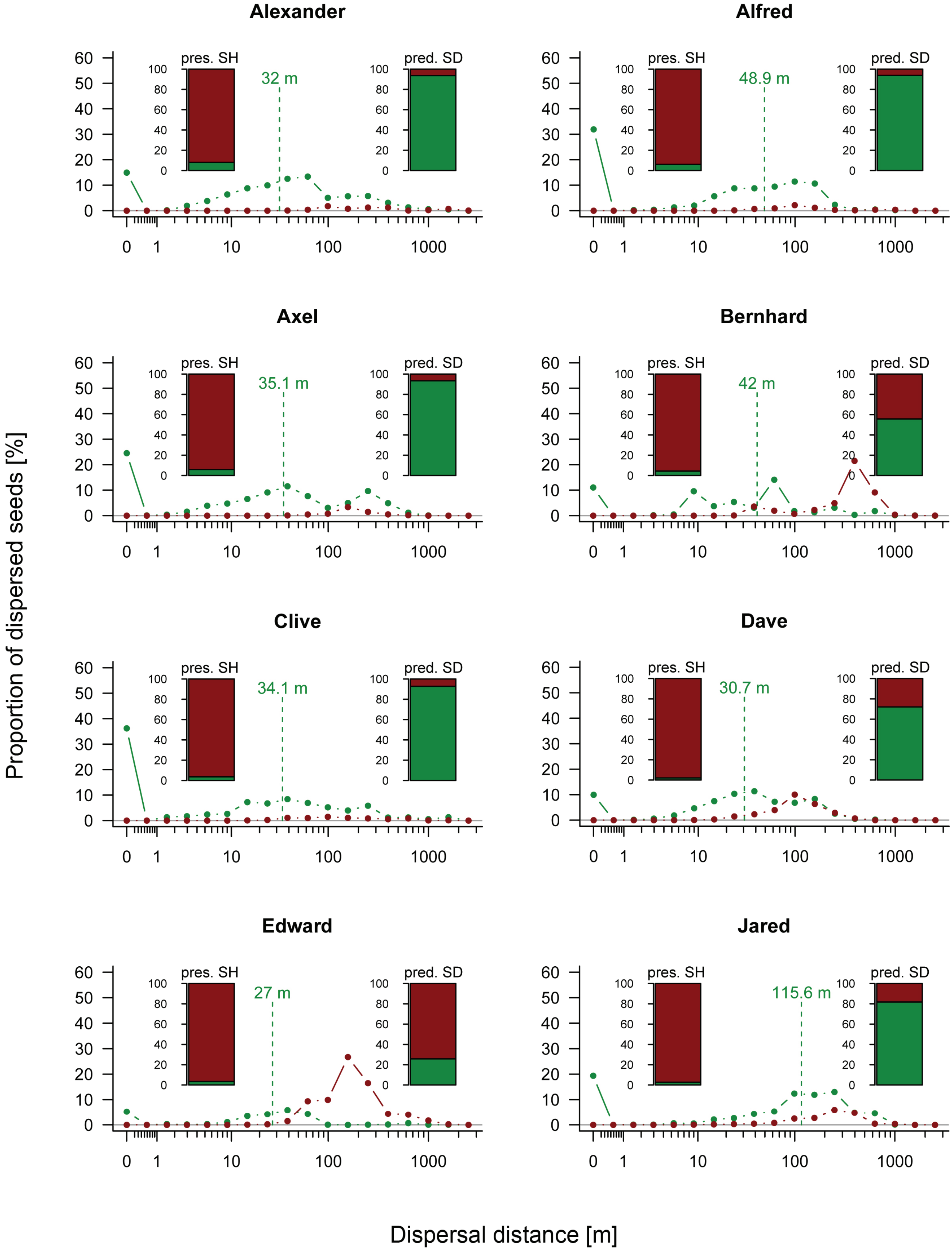


Figure A10.2: Individual-based seed-dispersal into suitable (*green*) and unsuitable (*red*) habitat for 21 farmland-dwelling Common Blackbirds with the median seed dispersal distance (*dashed line*). Bars indicate the proportions of present suitable habitat (*pres. SH*) inside the home range of each bird and the predicted seed dispersal (*pred. SD*) from the models into either suitable (*green*) or unsuitable habitat (*red*).

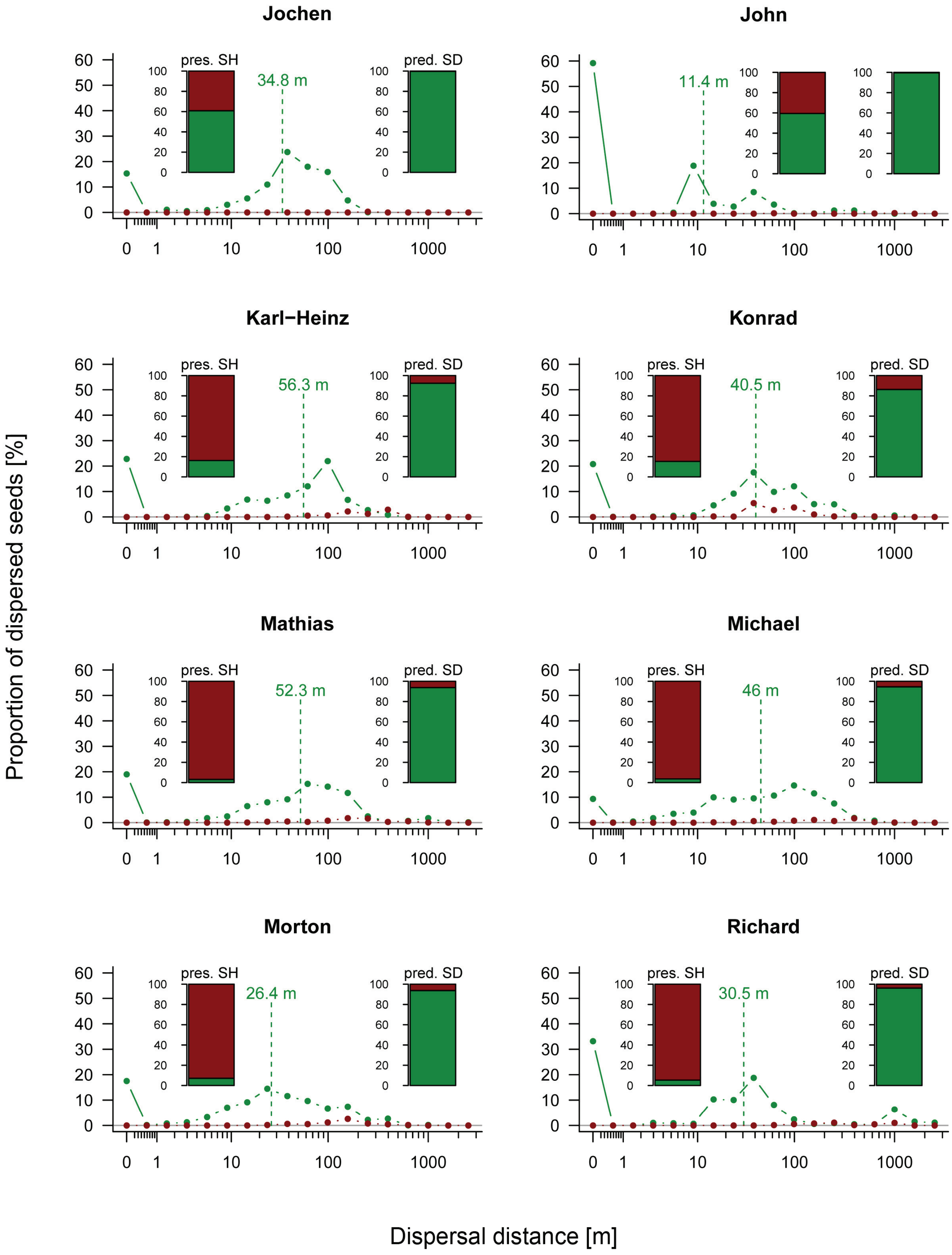


Figure A10.2 continued.

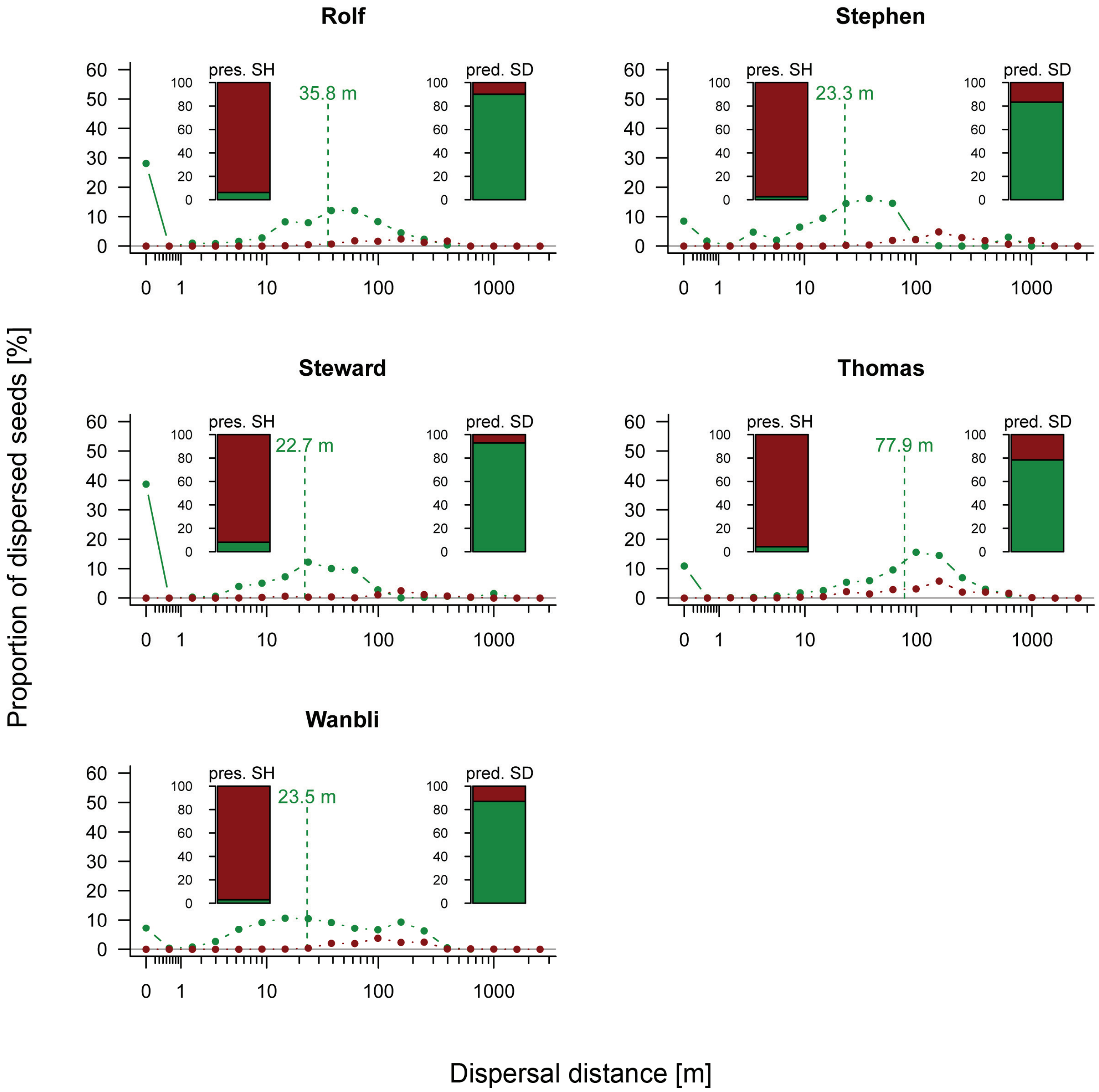


Figure A10.2 continued.

Table A10.3: Summary statistics of seed dispersal distances (SDDs) for each individual Common Blackbird. Additionally given are the proportions of present suitable habitat (pres. SH) within the home ranges of the blackbirds and the predicted seed dispersal (pred. SD) from the movement analyses. Extreme values are printed in *bold*.

Individual	**Median SDD [m]**	**Maximum SDD [m]**	**Proportion of locations in preferred habitat [%]**	**Proportion of habitat for pres. SH and pred. SD [%]**
Forest				
Albert	78.88	578.83	99.88	90.5 / **100.0**
Charles	**83.18**	1094.02	98.97	70.4 / 94.2
Colin	39.90	592.89	**100.00**	88.6 / 97.3
Ernst*	42.75	817.87	53.51	70.0 / 95.7
James	66.99	531.92	99.15	65.5 / 99.2
Justus	65.76	897.28	**100.00**	**98.4** / **100.0**
Paul	63.82	1244.36	98.40	78.4 / 99.6
Robert	73.79	807.01	87.75	81.8 / 98.9
Simon*	71.62	**1403.82**	55.08	27.5 / 81.3
Stefan	61.20	618.48	90.07	73.1 / **100.0**
Yanneck	80.82	672.51	**100.00**	95.7 / 99.3
Farmland				
Alexander	36.18	1718.02	**100.00**	8.0 / 93.6
Alfred	50.42	878.74	**100.00**	6.1 / 93.8
Axel	39.13	659.58	**100.00**	6.0 / 93.3
Bernhard	60.28	**2220.21**	88.84	4.4 / 55.7
Clive	38.99	1501.06	**100.00**	3.6 / 92.7
Dave	46.32	543.01	**100.00**	2.1 / 72.0
Edward	115.32	1261.97	**100.00**	3.4 / 25.8
Jared	**133.45**	724.57	**100.00**	2.7 / 81.8
Jochen	34.84	191.60	**100.00**	**60.8** / **99.7**
John	11.45	656.45	**100.00**	59.4 / 99.6
Karl-Heinz	64.06	438.25	**100.00**	16.2 / 92.4
Konrad	41.84	985.37	**100.00**	15.3 / 86.2
Mathias	56.24	1780.09	**100.00**	3.1 / 93.7
Michael	48.57	720.97	**100.00**	3.6 / 94.5
Morton	29.48	784.25	**100.00**	7.1 / 93.7
Richard	38.00	1734.81	85.51	5.3 / 96.1
Rolf	39.34	401.53	99.32	6.2 / 90.1
Stephen	28.72	933.87	**100.00**	2.5 / 83.3
Steward	28.64	940.52	80.15	8.1 / 92.8
Thomas	85.91	981.76	**100.00**	4.3 / 78.3
Wanbli	30.09	677.46	**100.00**	3.0 / 87.0

* These forest-dwelling birds were excluded from the habitat-specific analyses because they frequently switched between forest and farmland habitats.

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Zu gutter Letzt möchte ich den vielen Leuten danken, die mich während der gesamten Zeit meiner Promotion auf verschiedenste Art unterstützt haben und ohne deren Zuwendung, Hilfe und Rat diese Arbeit ganz sicher nicht möglich gewesen wäre – *Last but not least I would like to thank all the people who supported me while I was working on my PhD in Ecology and without whose attention, help and advice all this would surely not have been possible.*

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Curriculum Vitae

Name:	Nils Breitbach
Date of birth:	1st February 1977
Place of birth:	Wiesbaden, Germany
Nationality:	German
Address:	Biodiversität und Klima Forschungszentrum (BiK-F) Senckenberganlage 25 60325 Frankfurt am Main Germany www.bik-f.de
Email:	nils.breitbach@senckenberg.de

Academic education

11/2006–02/2012	**PhD-Thesis in Ecology**: “The impact of land-use intensification on pollination and seed-dispersal interactions in wild cherry (*Prunus avium* L.)”, Department of Ecology, Johannes Gutenberg-Universität Mainz, Germany (from 14th November 2006 – 14th August 2010) and Biodiversität und Klima Forschungszentrum (BiK-F), Projektbereich B3.10: Biogiversität und Arealdynamik von Vertebraten, Germany (from 15th August 2010 – 14th February 2012). Supervisor: Prof. Dr. Katrin Böhning-Gaese
13.11.2006	**Diploma-Thesis in Ecology**: "Landscape structure, bird diversity and seed dispersal of *Prunus avium*", Department of Ecology, Johannes Gutenberg-Universität Mainz, Germany. Supervisor: Prof. Dr. Katrin Böhning-Gaese
10/2000–11/2006	**Diploma courses in Biology** at the Johannes Gutenberg-Universität Mainz, Germany. Examinated subjects: Ecology/Zoology (main subject), Botany and Paleontology.
2002–2003	**Studying abroad** via ERASMUS, Institute of Biomedical and Life Sciences, University of Glasgow, UK.

Scholarships and Grants

2008–2011	"Stipendium Arten- und Biotopschutz", PhD-Scholarship from the Ministerium für Umwelt, Forsten und Verbraucherschutz (MUF) Rheinland-Pfalz, Germany.
2002–2003	SOCRATES/ERASMUS Programme, Scholarship for studying abroad at the University of Glasgow, Scotland.
2006	"Stipendium Arten- und Biotopschutz", Diploma-Scholarship from the Ministerium für Umwelt, Forsten und Verbraucherschutz (MUF) Rheinland-Pfalz, Germany.