

**Ökologische Untersuchung und
Bewertung der Extensivierung einer Hochweide:
Eine Fallstudie an Laufkäfern der Alpe Einödsberg im Allgäu**



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1 Zusammenfassende Darstellung der Arbeit

1.1 Einleitung

Der Schutz der biologischen Vielfalt stellt eine der bedeutendsten gesellschaftlichen Herausforderungen unserer Zeit dar. Zum 2010 ausgerufenen Jahr der Biologischen Vielfalt erklärte Bundeskanzlerin Merkel: „Die Frage der Erhaltung der biologischen Vielfalt hat dieselbe Dimension und Bedeutung wie die Frage des Klimaschutzes.“ (Merkel 2010). Bei allen Schwankungen, welche das Thema bezüglich seiner Gewichtung erfährt, hat sich an dem grundsätzlichen Konsens, dass der Schutz der Biodiversität ein gesamtgesellschaftliches Anliegen darstellt, nichts geändert (vgl. Weber 2018). Seit 2012 besteht das IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services) als Pendant zum Weltklimarat IPCC. Viele Nationen haben eine Biodiversitätsstrategie ausgearbeitet, und die EU hat Biodiversitätsziele für 2020 und eine Vision für 2050 formuliert (Publications Office of the European Union 2012).

Ungeachtet der Bedeutung des Themas sind wir aber immer noch weit davon entfernt, den Verlust der Biodiversität zu stoppen: „Trotz vielfältiger globaler Anstrengungen und zahlreicher Erfolge geht der Verlust an biologischer Vielfalt weiter. Der 4. Globale Bericht zur Lage der biologischen Vielfalt zeigt, dass wir unsere Anstrengungen national und international vervielfachen müssen, um die uns gesteckten Ziele bis 2020 erreichen zu können.“ (Sekretariat des Übereinkommens über die biologische Vielfalt 2014, S.1). Vermehrte Anstrengungen sind auf unterschiedlichen gesellschaftlichen Ebenen vonnöten (Armsworth et al. 2007; Rea, Munns 2017). Es wird betont, dass der Schutz der Biodiversität eine Querschnittsaufgabe darstellt (Europäische Kommission 2015).

Für alle diese Aspekte ist eine solide Datengrundlage zur Beurteilung der Situation der Biologischen Vielfalt und der einzelnen Arten sowie Kenntnis über Zusammenhänge (Ökosystemfunktionen) und Wirkungen von Veränderungen und Artenverlusten unabdingbar, um gerade auch Prognosen über Konsequenzen des menschlichen Handelns zu geben. Hier ist insbesondere die naturschutzfachliche Forschung gefragt.

Dass Forschungsergebnisse durchaus aktuelle politische Diskurse beeinflussen können, erleben wir aktuell an den vielfältigen Reaktionen auf eine Publikation zum Rückgang der Insekten (Hallmann

et al. 2017). Die zu Grunde liegende Untersuchung, initiiert von Mitgliedern des Krefelder Entomologischen Vereins, hat ein bemerkenswertes (auch internationales) Medienecho nach sich gezogen (z.B. Baier 2017; McKirdy 2017; Carrington 2017).

Dabei ist die Studie nur ein weiterer Hinweis auf den Prozess eines starken Rückgangs von Arthropoden, der in den letzten Jahrzehnten stattfindet. So haben Heydemann & Meyer (1983) bei der Wiederholung einer Untersuchung nach 30 Jahren Rückgänge von 50-80 % bei den Arten- und Individuenzahlen von Bodenarthropoden in intensiv genutzter Kulturlandschaft festgestellt. Habel et al. (2016) stellten einen Rückgang der Artenzahl um etwa 40% bei den tagaktiven Großschmetterlingen in der Region Regensburg im Lauf von 170 Jahren fest. Wenzel et al. (2006) konnten über 30 Jahre einen Rückgang von über 50% bei den stenöken Tagfalterarten auf Kalkmagerrasen in Südwestdeutschland feststellen. Bei Laufkäfern sind Rückgänge der Biomasse von über 40% in zwei Untersuchungsgebieten in den Niederlanden innerhalb der letzten 30 Jahre festgestellt worden (Hallmann et al. 2018).

Die Abnahme von Insekten und Arthropoden wird entsprechend unter Fachleuten schon länger als großes Problem erkannt (Baillie et al. 2012; Dirzo et al. 2014). Es wird betont, dass weitere Forschung und insbesondere die Vermittlung der Forschungsergebnisse für den notwendigen gesellschaftlichen Wandel zentral sind (Sekretariat des Übereinkommens über die biologische Vielfalt 2014; Dirzo et al. 2014; Kati et al. 2015).

Ein zentrales Element der bereits erwähnten Europäischen Biodiversitätsstrategie ist das Europäische Schutzgebietssystem Natura 2000 (EU 1992; Wurzel 2008; Orlikowska et al. 2016). Ziel des Schutzgebietssystems ist der langfristige Erhalt und die Wiederherstellung der biologischen Vielfalt in der Europäischen Union. Dazu wird ein günstiger Erhaltungszustand der natürlichen Lebensräume sowie von Tier- und Pflanzenarten angestrebt, mit dem Fokus auf Arten die charakteristisch für Europa sind (Ssymank et al. 1998; Vischer-Leopold et al. 2012).

Ein Europäisches Schutzgebietssystem muss insbesondere die hohen Bevölkerungsdichten und die lange Geschichte der anthropogenen Landnutzung in Europa berücksichtigen (Kati et al. 2015). Der Habitatverbund wird als ein zentrales Element beim Schutz der Biodiversität gesehen, insbesondere in Zeiten klimatischer Veränderungen. Daher ist offensichtlich, dass ein Schutzgebietssystem in Europa gerade auch die artenreiche Kulturlandschaft erhalten muss (Hampicke 2013).

Der Alpenraum wird zwar häufig als großflächiges Wildnisgebiet gesehen, in Wirklichkeit wurden die Ökosysteme der Alpen durch den Menschen bereits sehr früh umgestaltet (Bätzing 2005).

Insbesondere entlang der natürlichen Waldgrenze erfolgte eine frühe Besiedlung durch den Menschen. Die alpinen Rasen eigneten sich in ihrer natürlichen Form bereits als Weidegebiete und wurden schon frühzeitig durch transhumante Nutzungsformen erschlossen. Zur Erweiterung der Weidefläche wurde in weiten Teilen des Alpenraumes die Waldgrenze sukzessive gesenkt und große offene Flächen – gemähte Wiesen und vom Vieh geprägte Weiden – geschaffen (Heiri et al. 2006). Aufgrund dieser Kulturgeschichte und ihrer Lage als Hochgebirge mitten in Europa sind die Alpen ein einzigartiger und naturräumlich besonders diverser und dynamischer Landschaftsraum. Sie stellen einen von intensiv genutzter Agrarlandschaft umgebenen *hotspot* der Biodiversität in Europa dar und sind durch eine hohe Anzahl endemischer Tier- und Pflanzenarten charakterisiert (Rabitsch, Essl 2009).

Allerdings war die Kulturlandschaft im Alpenraum in den letzten Jahrzehnten einem besonders starken Strukturwandel ausgesetzt (Bätzing 2005). Als Region mit einem hohen Anteil an Grenzertragsstandorten lassen sich hier zwei gegenläufige Entwicklungen feststellen: zum einen findet eine Intensivierung der Landnutzung in Bereichen mit guter Zugänglichkeit und maschineller Nutzbarkeit statt, insbesondere in den Talauen. Zum anderen kommt es häufig zu einem Rückgang der Nutzung oder Nutzungsaufgabe in Bereichen, in denen die landwirtschaftliche Bearbeitung schwierig ist. Die Auswirkungen auf die Biodiversität werden bei beiden Entwicklungen kritisch gesehen (Bonavita et al. 1999; Tasser, Tappeiner 2002; Stöcklin et al. 2007). Grundsätzlich sind die Lebensraumtypen des Grünlands in der alpinen Region Deutschlands nicht in einem günstigen Erhaltungszustand (Vischer-Leopold et al. 2012).

Die Allgäuer Alpen gelten als das artenreichste Gebiet der Bayerischen Alpen (Haslach 2011). Im Jahr 1992 wurde daher das Naturschutzgebiet „Allgäuer Hochalpen“ eingerichtet, welches aktuell das drittgrößte Naturschutzgebiet Bayerns darstellt. Seit 2001 sind die Allgäuer Hochalpen als SPA („Special Area of Conservation“, EU 1992) geführt.

In diesem Schutzgebiet befindet sich die Einödsberg-Alpe, die etwa 15 km südlich von Oberstdorf nahe der südlichsten Siedlung Deutschlands Einödsbach, gelegen ist (Abb. 1).

Das beweidete Gebiet reicht östlich bis zum Grat vom Schmalhorn (1952 m ü. NN) im Norden und Wildengundkopf (2238 m) im Süden (Abb. 2, 3, 6). Von diesem Gratrücken ziehen sich die beweideten steilen Grasflanken abwärts nach Westen zur nördlich gelegenen Vorderen Einödsberg-Alpe (1647 m) bzw. zur südlichen Hinteren Einödsberg-Alpe (1555 m).

Zweifelsohne ist das Gebiet infrastrukturell schlecht erschlossen, es gibt keinerlei Fahrwege, so dass eine Belieferung entweder mit dem Helikopter erfolgen muss oder durch Aufstieg vom Stillachtal. Eine maschinelle Intensivierung ist auf den steilen Hanglagen ausgeschlossen.

Die steilen Hänge der Einödsberg-Alpe unter dem Wilden- und Spätengundkopf wurden Anfang des 20. Jahrhunderts gemäht und z. T. mit wenigen Rindern bestoßen (Enzensperger 1906). In der ersten Hälfte des 20. Jahrhunderts arbeiteten noch mehr als 10 Menschen landwirtschaftlich in dem Gebiet, die Alpe wurde als Sennerei mit Produktion von Butter und Käse geführt (H. Radeck pers. Mitteilung).



Abbildung 1: Lage des Untersuchungsgebiets im Süden Deutschlands. Maßstab 1 : 10 Mio.

Diese damalige Nutzung war extensiv, allerdings sehr arbeitsintensiv. Im Rahmen einer zunehmenden Industrialisierung der Landwirtschaft wurde diese Nutzungart aufgegeben und von

einer Beweidung mit Schafen abgelöst: seit den 70er Jahren und bis 1999 wurde das Gebiet zeitweise mit über 2000 Schafen beweidet (Abb. 4; Höfer et al. 2010). Zu der hohen Dichte an Nutztieren kam dabei noch eine geringe Lenkung durch Behirtung auf der großflächigen Standweide dazu, welche durch selektive Platzwahl der Tiere immer zu lokal deutlich stärkeren Tritt- und Frasseinfluss führt (Stöcklin et al. 2007). Diese intensive und teils unkontrollierte Be- und Überweidung durch die Schafe hat die Vegetation vor allem im Gratbereich stark verändert und degradiert (Höfer et al. 2010). Im Jahr 2000 wurde – auch auf Drängen des amtlichen Naturschutzes – eine kontroverse Diskussion über Änderungen der Nutzung im Gebiet geführt. Konkret stellte sich die Frage, ob noch Nutzung durch Beweidung stattfinden sollte, ob andere Pflege- oder Managementmaßnahmen notwendig wären, oder ob man das Gebiet sich selbst und damit einer natürlichen Sukzession überlassen sollte.

Dabei wurde beschlossen, im Rahmen eines Projekts extensive Beweidung mit Jungrindern auf einem großen Teil der Weidefläche zuzulassen und lediglich kleine Bereiche aus der Nutzung zu nehmen. Naturschutzfachliches Ziel war es, die Vegetation in einem großen Teil der subalpinen Rasen zu regenerieren und gleichzeitig eine traditionelle Nutzung zu erhalten. 2001 wurde erstmals im engeren Bereich zwischen Vorderer und Hinterer Einödsbergalpe mit 48 Stück Jungvieh beweidet, in den Jahren 2002 bis 2008 beweideten dann zwischen 70 und 120 Stück Jungvieh die Alpe (Abb. 5). Der Hirte H. Radeck praktizierte eine geplante und kontrollierte Weideführung durch variables Auszäunen, mit dem Ziel, die gesamte zur Verfügung stehende Weidefläche zu bestossen und Standweiden zu vermeiden.

Die wissenschaftliche Begleitung war ein wichtiges Element des Projekts Einödsberg. In diesem Rahmen wurden unterschiedliche Taxa bearbeitet, Schwerpunkte bildeten Untersuchungen der Vegetation sowie der Spinnentiere und Laufkäfer des Gebiets. Der Fokus dieser Dissertation liegt in den Untersuchungen der Laufkäfer.

Laufkäfer sind ein wichtiges Taxon bei der naturschutzfachlichen Bewertung von Gebieten (Luff 1996; Koivula 2011; Homburg et al. 2014). Sie reagieren deutlich auf Veränderungen der Landnutzung (Lövei, Sunderland 1996; Kotze et al. 2011) und sind daher für die Evaluation von Naturschutzmaßnahmen gut geeignet. In den Alpen weisen sie zudem einen hohen Anteil endemischer Arten auf (Paill, Kahlen 2009) und sind daher eine wichtige Gruppe für Betrachtungen der Biodiversität. Während die Laufkäfer der Alpen in Österreich und der Schweiz gut bearbeitet sind (z.B. Holdhaus 1954; Franz 1970; Marggi 1992; Luka 2009; Paill, Kahlen 2009) liegen aus

Deutschland kaum systematische Untersuchungen vor (Gesellschaft für Angewandte Carabidologie 2009).

Im Rahmen der Dissertation sollten mehrere Fragen bearbeitet werden.

- Es sollte ein geeignetes Erfassungsschema für Laufkäfer in schwer erreichbaren Gebieten der Alpen erstellt werden, um überhaupt intensive und mehrjährige Untersuchungen durchführen zu können. Aufgrund des hohen Aufwands bei der Fallenleerung auf der Alpe Einödsberg (Laufstrecke von über 30km mit mehr als 1000m Höhenunterschied) war ein Anliegen, die Anzahl der Fallenleerungen zu reduzieren. Als Arbeitshypothese wurde angenommen, dass eine im Vergleich zum Tiefland geringere Anzahl an Fallenleerungen in Hochgebirgsökosystemen aufgrund einer stark verkürzten Aktivitätszeit von Laufkäfern zu gut interpretierbaren und repräsentativen Ergebnissen führt.
- Des Weiteren sollte untersucht werden, inwieweit die Einbeziehung der Laufkäfer in die Untersuchungen zusätzliche Erkenntnisse zu anderen Taxa im Gebiet erbringt. Als Hypothese wurde angenommen, dass in einem so heterogen strukturierten Gebiet mit hoher Standortvielfalt und starken Nutzungsunterschieden verschiedene Taxa unterschiedliche Reaktionen auf Veränderungen zeigen und speziell die Laufkäfer eine wichtige Ergänzung zu einer Auswertung der Vegetation darstellen.
- Das zentrale Anliegen der Studie bestand darin, die Reaktion der Laufkäfer auf die Nutzungsänderung aufzuzeigen. Hier wurde von einem negativen Einfluss der ehemaligen intensiven Nutzung und daher von einer positiven Gesamtentwicklung nach der Nutzungsextensivierung ausgegangen.

Im Rahmen des Projekts sind die bisher intensivsten Laufkäferuntersuchungen im deutschen Alpengebiet durchgeführt worden. Bei einigen der nachgewiesenen Arten, z.B. *Oreonebria picea* oder *Amara nigricornis*, handelt es sich um die größten Aufsammlungen in Deutschland, die damit auch für andere carabidologisch arbeitende Wissenschaftler von Interesse sind. Daher wurde auch eine kommentierte Artenliste des Gebiets publiziert, um die Erkenntnisse zur Verbreitung der Laufkäferarten in den Alpen einem breiten Kreis zur Verfügung zu stellen (Harry, Höfer 2010). Die Publikation ist frei verfügbar und sei jedem ans Herz gelegt, der sich für die faunistischen Daten des Gebiets interessiert. In dem gleichen Band befindet sich auch eine Beschreibung sämtlicher beprobter Standorte des Projekts inklusive Koordinaten (Höfer et al. 2010). Eine Auflistung der für Kapitel 3 bis 5 relevanten Standorte gibt Tabelle 1.1.

Tabelle 1.1: Lage der Untersuchungsstandorte. Die Standorte, welche mit V und X beginnen, sind am Einödsberg bzw. in unmittelbarer Umgebung. Die Standorte AS04, BG01 und SL02 sind Vergleichsstandorte in den Allgäuer Alpen. Die Spalten Kap. 3, Kap. 4 und Kap. 5 geben an, in welchen Beiträgen die jeweiligen Standorte ausgewertet wurden. Eine detaillierte Standortbeschreibung ist in Höfer et al. (2010) einsehbar.

Standort	Höhe (m NN)	Lat W (WGS84)	Lon N (WGS84)	Kap. 3	Kap. 4	Kap. 5
V 01	1562	10.277465	47.320020		x	
V 02	1875	10.289272	47.327924	x	x	x
V 03	1880	10.289215	47.328084	x	x	x
V 05	1885	10.288665	47.329632	x	x	x
V 06	1751	10.285017	47.327704	x	x	x
V 08	1776	10.286376	47.328180	x	x	x
V 10	1809	10.285255	47.318110	x	x	
V 11	1703	10.281607	47.317648	x	x	x
V 12	1525	10.278865	47.320858		x	
V 13	1535	10.280088	47.322102		x	
V 14	1542	10.276370	47.317091		x	x
V 15	1580	10.281802	47.321720		x	
V 16	1790	10.285879	47.322819	x	x	
V 23	1765	10.284293	47.318994	x	x	x
V 26	1768	10.285146	47.317835		x	
X 01	1884	10.288484	47.329938	x		x
X 03	1896	10.287001	47.318426	x		x
X 04	1980	10.288880	47.318486	x	x	x
X 05	1993	10.289161	47.318736	x	x	x
X 06	1754	10.284742	47.320360			
X 07	1781	10.287147	47.325513	x		x
X 08	1786	10.287098	47.326205	x		x
X 09	1798	10.286868	47.328635	x		x
X 10	1911	10.287809	47.320286	x		x
X 11	1751	10.283944	47.319181	x	x	x
X 13	1750	10.285675	47.324732	x		
X 14	1565	10.281156	47.324128	x		
X 15	1550	10.280687	47.324535	x		
X 17	1434	10.276965	47.327438	x	x	
X 18	1476	10.277986	47.327802	x	x	
X 19	1631	10.282580	47.329018		x	
X 20	1720	10.282306	47.318186	x	x	x
X 21	1990	10.289117	47.317372	x	x	x
AS 04	1786	10.356222	47.357639		x	
BG 01	1941	10.393528	47.405778		x	
SL 02	1939	10.233511	47.361714		x	



Abbildung 2 und 3: Ansichten des Untersuchungsgebiets, eine Aufnahme im Frühjahr vom Grat aus, eine Aufnahme im Spätsommer mit einigen Untersuchungsflächen.



Abbildung 4 und 5: Schafbeweidung Ende der 1990er Jahre an der Hinteren Alphütte. Aktuell wird ein großer Teil der Fläche extensiv von Rindern beweidet

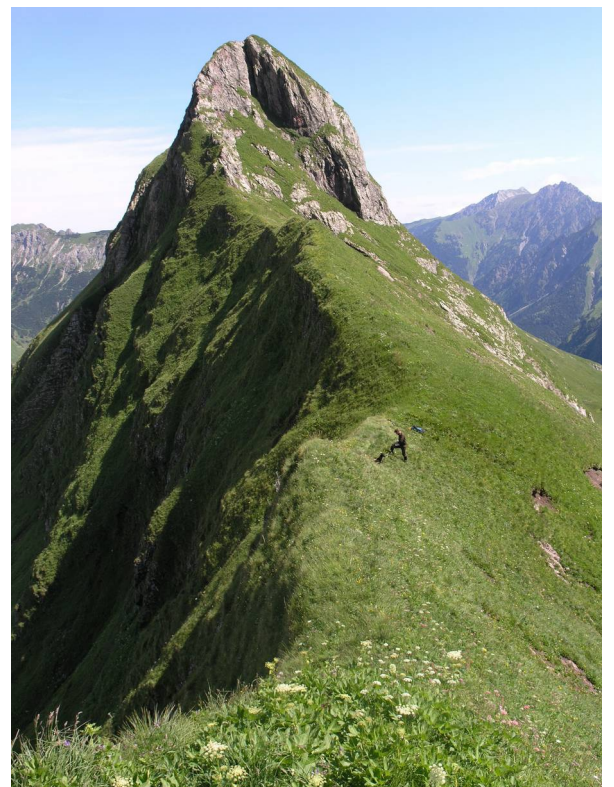


Abbildung 6 und 7: Da der Weideeinfluss an den Gratlagen der Alpe Einödsberg sehr stark ist (Abb. 6) wurden zusätzliche unbeweidete Vergleichsflächen beprobt, wie am Bergächtele (Abb. 7).

1.2 Zusammenfassung der einzelnen Beiträge

1.2.1 Beitrag 1: *When to sample in an inaccessible landscape: a case study with carabids from the Allgäu (northern Alps) (Coleoptera, Carabidae)*

Laufkäfer gelten als gut geeignete Gruppe zur Klärung vieler ökologischer Fragestellungen. Eine Standardmethode zur Erhebung von Laufkäferdaten sind Bodenfallen. Die Fangergebnisse lassen sich dabei gut auswerten. In Hochgebirgen gibt es bisher allerdings nur sehr wenig Untersuchungen mit Bodenfallen (Brandmayr et al. 2003; Gesellschaft für Angewandte Carabidologie 2009). Als Hauptursache ist der hohe Aufwand bei der Installation und regelmäßigen Leerung aufgrund der schwierigen Erreichbarkeit der Untersuchungsgebiete zu sehen. Um die Untersuchung von Laufkäfern in Hochgebirgen voranzutreiben wäre eine Möglichkeit, die Anzahl an Erfassungsintervallen zu reduzieren. Durch die Reduktion der Probenanzahl wird auch die Anzahl erfasster Laufkäferindividuen und wahrscheinlich auch -arten reduziert. Daher ist ein Verständnis über den Zusammenhang zwischen reduziertem Erfassungsaufwand und erfasster Artenzahl wichtig, um Zeiten und Häufigkeiten von Beprobungen festzulegen sowie die Belastbarkeit reduzierter Stichprobensätze zu überprüfen.

Für die Untersuchung wurden im Jahr 2005 an 25 Standorten über die gesamte Vegetationsperiode von Anfang Juni bis Ende September Bodenfallen installiert. Die Phänologien unterschiedlicher Arten wurden ausgewertet und die Ergebnisse von dem gesamten Fangzeitraum wurden mit denen reduzierter Erfassungsintervalle verglichen.

Insgesamt konnte bei den meisten Laufkäferarten ein ausgeprägter Frühjahrspeak im Juni festgestellt werden. Wenige Arten zeigten einen verspäteten Aktivitätspeak im Juli, und einzelne Arten hatten keinen klaren Hauptaktivitätszeitraum. Der Frühjahrspeak war insgesamt in den hohen Lagen des Untersuchungsgebiets am stärksten ausgeprägt. Arten mit einer Hauptaktivitätszeit im Spätsommer oder Herbst, wie sie in den Tieflagen angetroffen werden, waren im Gebiet nicht vorhanden. Dies deckt sich mit Beobachtungen anderer Untersuchungen im Hochgebirge (z.B. de Zordo 1979; Gereben 1995; Luka 2009). Aufgrund der kurzen Vegetationsperiode ist ein schneller Beginn der Reproduktion wichtig. Dies gilt umso mehr, da die Larvalentwicklung bei den niedrigen Durchschnittstemperaturen in Hochgebirgen länger dauert (Paarmann 1966; Ferenz 1975). Dabei sind die Bedingungen direkt nach der Schneeschmelze für die Laufkäferarten sehr

gut: der Boden ist feucht, die Temperaturen sind bereits hoch und der Raumwiderstand (Heydemann 1956) ist aufgrund der noch niederliegenden Vegetation gering.

Aufgrund der festgestellten Phänologien wurden die Ergebnisse der gesamten Vegetationsperiode mit den Ergebnissen einer auf zwei Erfassungsintervalle reduzierten Erhebung verglichen. Die beste Abdeckung der aufgetretenen Artenzahlen pro Standort brachte die Kombination von erstem und drittem Erfassungsintervall, also der ersten Junihälfte unmittelbar nach der Schneeschmelze an den oberen Standorten, und der ersten Julihälfte.

Ein Vergleich der Klassifikation des gesamten Datensatz mit dem vorgeschlagenen Mindestprogramm zeigt, dass der reduzierte Datensatz den gesamten Zeitraum hinreichend repräsentiert. Zudem wird bei dem reduzierten Datensatz ein höherer Anteil an Arten nachgewiesen, als in den Tieflagen bei einer Reduktion auf das dort vorgesehene Erfassungsprogramm (Trautner 1992; Duelli et al. 1999).

1.2.2 Beitrag 2: Protected habitats of Natura 2000 do not coincide with important diversity hotspots of arthropods in mountain grasslands.

Biodiversitätserfassungen sind ein zentrales Element im Naturschutz und werden z.B. zur Abgrenzung von Schutzgebieten, im Monitoring oder für Planung und Evaluation von Schutzmaßnahmen genutzt. Zeit und Geld sind für die Erfassungen immer ein limitierender Faktor. Als mögliche Lösung wird der Ansatz von Surrogaten diskutiert. Darunter versteht man die Übertragung der Ergebnisse eines begrenzten Artensets auf andere Arten (Taxa) (Noss 1990; Prendergast et al. 1993). Dieser Ansatz wird auch im Kontext von Natura 2000 angewandt: Hier fokussieren Schutzbemühungen auf Lebensraumtypen, welche fast ausschließlich über die Vegetation definiert sind (Europäische Kommission, DG Environment 2013) sowie auf ein sehr begrenztes faunistische Artenset welches in den Anhängen der Vogelschutzrichtlinie und FFH-Richtlinie genannt ist.

Die Funktion von Surrogaten wird allerdings immer noch diskutiert. Hauptkritik an dem Ansatz ist, dass die Kongruenz von Veränderungen und damit die Übertragbarkeit auf andere Gruppen häufig nicht gegeben ist (Favreau et al. 2006; de Morais et al. 2018).

Im Projekt Einödsberg haben wir untersucht, ob die Vegetation als Surrogat für die beiden untersuchten Arthropodengruppen (Spinnentiere und Laufkäfer) dienen kann. Dies wurde sowohl auf Ebene der Artzusammensetzung (über multivariate Ordination) als auch des Artenreichtums für die drei Taxa geprüft. Zudem wurde überprüft, ob die unter vegetationskundlichen Aspekten

abgegrenzten geschützten Lebensraumtypen auch tatsächlich wertvolle Habitats für die Arthropodengruppen darstellen.

Dafür wurden auf insgesamt 26 Grünlandstandorten alle drei Gruppen erfasst und die Daten verglichen.

Die Untersuchungen ergaben nur schwache Korrelationen der Artzusammensetzung der Gruppen und keine positiven Korrelationen beim Artenreichtum, hier ergab sich sogar ein negativer Zusammenhang zwischen Laufkäfern und Pflanzen. Die geschützten Lebensraumtypen decken bei der Vegetation die artenreicheren Standorte ab, nicht aber bei den Spinnen oder Laufkäfern.

Insbesondere die Standorte am Grat, welche aus vegetationskundlicher Sicht stark verarmt sind, stellen sich als für die Bodenarthropoden artenreiche Habitats mit einem hohen Anteil wertgebender Arten dar.

Die Ergebnisse der Untersuchung zeigen, dass eine ausreichende Kongruenz nicht gegeben und damit die Übertragbarkeit von Ergebnissen bei der Vegetation auf die untersuchten Arthropodengruppen in den Gebirgslebensräumen nicht gewährleistet ist. Die starken kleinräumigen Unterschiede in Nutzungsintensität, Topografie, dem Mikroklima und weiterer Faktoren beeinflussen die Lebensgemeinschaften der untersuchten Gruppen sehr kleinräumig und auf unterschiedliche Weise.

Ein breiter Ansatz zur Beantwortung von Naturschutzfragen in Gebirgen wird in dem Beitrag als erforderlich erachtet. Dies gilt insbesondere auch im Kontext von Natura 2000. Dabei werden die arten- und endemitenreichen Laufkäfer in den Alpen (Paill, Kahlen 2009) als sehr gut geeignete Ergänzung zu vegetationskundlichen Untersuchungen angesehen.

1.2.3 Beitrag 3: Recovery of carabid beetle assemblages after cessation of intensive grazing in the German Alps: A six year study.

Auf die besondere Stellung der Alpen in Mitteleuropa und den aktuell stattfindenden Strukturwandel ist bereits in der Einleitung hingewiesen worden. Im dritten Artikel wurde mittels gemischter Modelle (*mixed effects models*) untersucht, welche Veränderungen bei den Laufkäfern nach der Nutzungsänderung am Einödsberg auftraten. Modelle wurden für Arten- und Individuenzahlen, die Biomasse sowie die Eigenschaften (*traits*) Körpergröße, Flugfähigkeit, Bindung an Gebirge und Ernährungsweise (hier Vorkommen herbivorer Laufkäfer) gerechnet. In den Modellen wurde neben der allgemeinen Entwicklung über die Zeit auch auf Unterschiede der Entwicklung zwischen Standorttypen und aktuellen Weideflächen bzw. Brachen gesucht.

Sämtliche errechneten Modelle zeigten Veränderungen der abhängigen Variablen über die Zeit: nach Aufgabe der intensiven Schafbeweidung nahmen die Arten- und Individuenzahlen sowie die Biomasse an Laufkäfern zu. Die Tiere wurden durchschnittlich größer und es traten mehr herbivore Laufkäfer auf. Der Anteil an Gebirgsarten sowie an flugunfähigen Arten nahm zwar mit der Zeit ab, nicht aber die Abundanzen dieser Gruppen, welche mit der Zeit zunahmen.

Auch konnten unterschiedliche Entwicklungen zwischen den Standorten beobachtet werden: Während auf den Gratstandorten die Körpergröße stärker zunahm, stieg der Anteil an herbivoren Laufkäfern auf den Hängen. Für die Flugfähigkeit konnten gegenläufige Trends beobachtet werden: am Grat nahm der Anteil flugfähiger Arten zu, dagegen sank ihr Anteil in den Borstgrasrasen der Hänge. Die Zunahme der Körpergröße, Biomasse und des Anteils an Herbivorie läuft an den aktuellen Bracheflächen schneller ab als auf der Weide.

Die beobachteten Veränderungen werden im Artikel detailliert diskutiert. Die meisten Veränderungen, insbesondere die Zunahme der Artenzahlen sowie der durchschnittlichen Körpergröße, deuten auf eine Erholung der Laufkäferfauna von der intensiven Schafbeweidung hin und werden positiv bewertet. Dabei vollziehen sich die Veränderungen an den stärker devastierten Gratstandorten sowie auf den aktuellen Brachen schneller als am Hang bzw. auf den aktuell beweideten Flächen. Je größer der Gradient der Nutzungsänderung ist, umso schneller vollzieht sich die Veränderung.

Eine Veränderung, welche nicht in das Bild passt, ist die Abnahme des Anteils typischer Gebirgsarten. Zwar nimmt die Abundanz von Gebirgstieren zu, allerdings in geringerem Maße als die Abundanz von euryöken Arten, welche auch in tieferen Lagen vorkommen. Dies könnte ein Indiz für eine durch Klimaerwärmung induzierte Veränderung der Höhenverbreitung von Arten sein, wie sie von Brandmayr (2016) für die italienischen Alpen nachgewiesen wurde.

Die Extensivierung der Landnutzung ist naturschutzfachlich für die Laufkäfer positiv zu bewerten. Dabei zeigt die Auflassung der Nutzung über den Untersuchungszeitraum sehr gute Ergebnisse. Mittelfristig ist allerdings auf den Brachestandorten der unteren und mittleren Lagen der Alpe mit dem Aufkommen von Gehölzen zu rechnen, was zu einem Rückgang der Artenvielfalt führen dürfte (Bonavita et al. 1999; Tyler 2008). Eine extensive Beweidung, welche die hochmontanen und subalpinen Offenstandorte erhält, erscheint daher als naturschutzfachlich beste Pflegevariante für die Flächen.

Die hohe Anzahl signifikanter Zusammenhänge in den errechneten Modellen ist auch im Vergleich zu anderen Studien überraschend. Ein wichtiger Grund dafür ist die lange Untersuchungszeit. Es gibt kaum Studien, die über 5 oder mehr Jahre die gleichen Flächen untersuchen (van Klink et al. 2015). Populationsgrößen von Laufkäfern unterliegen aber erheblichen Schwankungen (den Boer

and van Dijk 1994), so dass bei kurzen Untersuchungen kaum zwischen jährlichen Schwankungen und realen Trends zu unterscheiden ist.

1.3 Fazit

Die durchgeführte sechsjährige Untersuchung ist meines Wissens die umfangreichste carabidologische Begleitung einer Nutzungsumstellung auf Weideflächen in Deutschland. Im deutschen Alpenraum ist sie bezüglich der Untersuchungsintensität herausragend. Ein intensiver Untersuchungsansatz kann aus Sicht des Naturschutzes per se als erfreulich gesehen werden, zeigt er doch dass das Thema ernst genommen wird. Auf der anderen Seite darf aufgrund der begrenzten Gelder im Naturschutz (inklusive der naturschutzfachlichen Forschung) durchaus gefragt werden, ob sich der Aufwand gelohnt hat.

Aus meiner Sicht geben die Ergebnisse dem gewählten Ansatz recht. Sie ermöglichen die fundierte Kritik rein vegetationskundlicher naturschutzfachlicher Erhebungen in den Alpen, wie sie sowohl im Rahmen von Managementplanungen für die FFH-Richtlinie als auch bei der Bayerischen Alpenbiotopkartierung überwiegend durchgeführt werden. Für Laufkäferuntersuchungen in den Alpen schlagen wir ein reduziertes Erfassungsprogramm vor, welches wir prinzipiell als geeigneten Mindeststandard für zukünftige Untersuchungen in den Hochlagen der Alpen sehen. Und wir konnten eine gut abgesicherte Bewertung der Nutzungsumstellung in unserem Untersuchungsgebiet abgeben, die auch für die Erfolgskontrolle von finanziell gewichtigen Agrarumweltprogrammen essentiell ist.

Eine wichtige Frage ist die nach der Übertragbarkeit der Ergebnisse. Hier sind insbesondere die edaphischen Bedingungen zu berücksichtigen, tiefgründige Mergel wie im Untersuchungsgebiet sind in erster Linie im umgebenden Allgäu zu finden (Scholz 1995). Ein Vergleich mit den wenigen Untersuchungen auf anderen Weideflächen in den Alpen legt allerdings nahe, dass eine extensive Weidenutzung auch bei anderer Geologie und Höhenlage naturschutzfachlich spannende Flächen produziert, wobei sich die Ergebnisse in Details durchaus unterscheiden (vgl. Kapitel 4.5).

Diese Arbeit möchte nicht den Anspruch stellen, das Thema Alpwirtschaft und Laufkäfer abschließend bearbeitet zu haben. Vielmehr sehe ich die Ergebnisse als eine wichtige Vorlage und fundierte Begründung, gerade auch im Alpenraum verstärkt Laufkäfer bei der Beantwortung naturschutzfachlicher Fragestellungen einzubinden.

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2 Übersicht der Beiträge und Anteil der Autorenschaft

Tabelle 2.1: Übersicht über die Beiträge, die in dieser Dissertation enthalten sind, mit der Nennung des eigenen Beitrags an jeder Studie (inkl. Gewichtungsfaktor nach §§9 und 12 der Richtlinie zur kumulativen Dissertation) sowie dem Publikationsstatus (IF= 2016 Impact factor im ISI Web of Knowledge).

Bei- trag	Titel	Autoren	eigener Beitrag	Gewich- tungs- faktor	Publikationsstatus
1	When to sample in an inaccessible landscape: a case study with carabids from the Allgäu (northern Alps) (Coleoptera, Carabidae)	Harry, Ingmar Drees, Claudia Höfer, Hubert Assmann, Thorsten	überwiegender Anteil	1	Veröffentlicht in <i>Zookeys</i> 100: 255-271. DOI: 10.3897/zookeys.100.1531 IF=1,079
2	Protected habitats of Natura 2000 do not coincide with important diversity hotspots of arthropods in mountain grasslands.	Harry, Ingmar Höfer, Hubert Schielzeth, Holger Assmann, Thorsten	überwiegender Anteil	1	Veröffentlicht in <i>Insect Conservation and Diversity</i> 12: 329-338. DOI: 10.1111/icad.12349 (IF=2,091)
3	Recovery of carabid beetle assemblages after cessation of intensive grazing in the German Alps: A six year study.	Harry, Ingmar Höfer, Hubert Schielzeth, Holger Assmann, Thorsten	überwiegender Anteil	1	Manuskript

Tabelle 2.2: Arbeiten der jeweiligen Autoren für die dieser Arbeit zugrunde liegenden Beiträge. Dabei setzen sich die verwendeten Kürzel aus den Anfangsbuchstaben der Autoren zusammen (siehe unten). Die Autoren sind gemäß ihres Arbeitsanteils an den Entstehungsschritten der Artikel angeordnet.

	Beitrag 1	Beitrag 2	Beitrag 3
Konzeption des Forschungsansatzes	IH	IH, HH, TA	IH, HH
Entwicklung der Forschungsmethoden	IH, HH, TA	IH, HH, TA	IH, HH
Durchführung der Forschung	IH	IH	IH
Erhebung und Aufbereitung der Daten	IH	IH, HH	IH, HS
Analyse/Interpretation von Daten und Zwischenergebnissen	IH, HH, TA, CD	IH, TA, HH, HS	IH, HS
Schreiben des Manuskripts	IH	IH	IH
Inhaltliche Überarbeitung des Manuskripts	IH, TA, HH, CD,	IH, HS, HH, TA	IH, TA, HH, HS

IH= Ingmar Harry^{1,2}, CD= Claudia Drees³, HH=Hubert Höfer⁴, HS=Holger Schielzeth⁵, TA=Thorsten Assmann¹

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Ich versichere, dass alle in diesem Anhang gemachten Angaben jeweils einzeln und insgesamt vollständig der Wahrheit entsprechen.

Ingmar Harry

3 Beitrag 1: When to sample in an inaccessible landscape: a case study with carabids from the Allgäu (northern Alps) (Coleoptera, Carabidae)

publizierter Artikel

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3.1 Abstract

While pitfall trapping is generally accepted as the standard method of sampling carabid beetles, this method has rarely been used in mountain ecosystems, mainly due to the high labour intensity it involves. As part of a research project in the German Alps, we investigated the phenologic appearance of adult carabid beetles in mountain ecosystems along with the consequences of possible reductions in sampling periods. Our results show that an early activity peak among carabids is predominant in mountain ecosystems. However, there are differences among species: the main group of species showed the highest activity directly after snow melt, a second group showed a delayed activity peak and a small third group had no clear peak at all. Based on this study, we recommend two fortnightly sampling periods as a minimum for a sampling programme: one immediately after snow melt, and a second sampling period after a pause of two weeks.

3.2 Introduction

Since harsh abiotic conditions along with high spatial heterogeneity dominate across mountain ecosystems, in stark contrast to the surrounding landscapes, alpine sites are interesting for ecological and biogeographical research (Lomolino 2001). This is especially true for questions related to environmental changes (e.g. climate change or change of land use) with mountains serving as suitable model ecosystems (Haslett 1997).

Carabid beetles are a group often used as indicator and/or model organism (Dufrene and Legendre 1997; Rainio and Niemela 2003; Szyszko et al. 2000). They have also been used to help understand fundamental ecological processes in mountain landscapes (e.g. Franz 1970; Holdhaus 1954).

Nevertheless, very few investigations have been carried out using pitfall traps in high elevation mountain areas (cf. Brandmayr et al. 2003a; Gesellschaft für Angewandte Carabidologie 2009), although this method is otherwise very widely used. The most cited reason given for the limited use of this method is that of labour intensity due to the difficulty in accessing these often remote study areas. To reduce the time invested, depending on the research issue, it might be possible to shorten the sampling period. A likely side effect will be a lower number of specimens captured, leading most probably to a reduction in the number of recorded species. An understanding of the relationship between reduced sampling effort and number of recorded species is needed as a basis

for decisions regarding timing and frequency of sampling, especially in the context of long-term monitoring.

Annual rhythms of activity and reproduction have been a major issue in carabidology, dating back to Larsson's pioneering work in this field (Larsson 1939). His classification of carabids' annual rhythms was elaborated upon and modified by other carabidologists (Lindroth 1949; Thiele 1977), and the importance of reproductive behaviour as a life history trait in carabids was emphasized by den Boer and van Dijk (1998) and Paarmann (1979). Many studies have dealt with the relationship between activity patterns and habitat preference, and these studies have led to a better understanding of distribution trends and specific habitat adaptations of carabids (den Boer and van Dijk 1996; Fahl and Purvis 1998; Hutchison 2007; Lys and Nentwig 1991; Matalin 1997; Riddick and Mills 1995; Traugott 1998).

For mountain ecosystems, the literature covering the reproductive seasonality of ground beetles is sparse. There are some works dealing with the phenology of carabids at high altitudes (De Zordo 1979a; b; Gereben 1995; Hosoda 1999; Janetschek et al. 1987; Lang 1975; Ottesen 1996; Sharova and Khobrakova 2005; Sota 1996). Many of these report a shortened activity period, but none of them examine possibilities and consequences of reduced sampling time.

A long-term research project in the "Allgäuer Hochalpen" in the German Alps was conducted in an area protected under the European Union "Habitats Directive". The project aimed at assessing effects of intensive long-term grazing of sheep and associated grazing regime changes after extensive cattle pasturing in 2000. In this project, intensive sampling of epigeic arthropods was performed over 6 years using pitfall traps. In this paper we focus on the seasonal activity of carabid beetles, primarily in the subalpine, but also in the alpine research area. We (1) describe the phenology of carabid beetles in the mountain ecosystems; and (2) investigate the consequences of reducing the number of sampling periods in order to present an optimized sampling scheme for recording the maximum number of species in subalpine and alpine altitudes of the northern Alps.

3.3 Methods

3.3.1 Study area

The mountain pasture "Alpe Einödsberg" (10,28°; 47,32°) is located in the German Alps (south-western Bavaria) and is part of the "Allgäuer Hochalpen", an area protected under the European Union "Habitats Directive". The study area ranges in altitude from 1400 to 2000 meters above sea level (m a. s. l.) and encompasses a total area of about 2 km². Most of the predominantly west-

facing slopes consist of meadows dominated by *Nardus stricta*. Woodland belts dominated by Norway spruce (*Picea abies*) and krummholz made up of *Alnus viridis*, occur throughout the pasture zone (Fig. 3.1). There is a 2 km ridge running north-south along the upper segment of the pasture. Additional information about the vegetation and geology is given in Höfer et al. (2008), Höfer et al. (2010) and SMNK 2009.



Figure 3.1: The study area “Alpe Einödsberg”. Position of some sampling sites is indicated with blue text.

In 2005, sampling was conducted at 25 sites. Sampling was focused on *Nardus stricta*-dominated meadows on slopes and on ridge sites dominated by *Deschampsia cespitosa*. In addition, several forest sites and open sites at lower altitudes were sampled (Table 3.1).

Table 3.1: Sample sites. Altitude is given in m a. s. l., incline and exposition in °.

site	type	altitude	inclination	exposition
V02	ridge	1875	12	180
V03	ridge	1880	21	210
V05	ridge	1885	29	275
V06	slope	1751	34	255
V08	slope	1776	35	260
V10	slope	1809	38	235
V11	slope	1703	27	250
V16	surface erosion	1790	35	230
V23	sucession <i>Alnus viridis</i>	1765	38	300
X01	ridge	1884	25	250
X03	slope	1896	33	270
X04	ridge	1980	32	280
X05	ridge	1993	9	250
X07	slope	1781	39	265
X08	slope	1786	35	260
X09	slope	1798	37	255
X10	ridge	1911	28	275
X11	slope	1751	34	300
X13	<i>Alnus viridis</i> krummholz	1750	38	320
X14	forest	1565	24	270
X15	forest	1550	34	285
X17	open, low altitude	1434	24	245
X18	open, low altitude	1476	31	270
X20	slope	1720	31	300
X21	ridge	1990	5	280

3.3.2 Sampling

At each sampling site, 6 pitfall traps (with a diameter of 6 cm, filled with 10% acetic acid, 90% water) were installed at a distance of 6 m from each other. In order to protect the traps from heavy rain and from cattle-related damage, traps were placed in a metal tube with a transparent plastic cover (Lederbogen et al. 2004).

The pitfall traps were installed at the beginning of June, just after the first snowmelt at the ridge, and were removed at the end of September 2005 after a period of snow cover. Traps were emptied every fortnight. Altogether, there were 8 sampling periods, these were numbered chronologically (1: June 5th – 18th, 2: June 19th – July 2nd, 3: July 3rd – July 18th, 4: July 19th – August 1st, 5: August 2nd – August 15th, 6: August 16th – August 29th, 7: August 30th – September 12th, 8: September 13th – September 26th).

Carabids were identified to species level; the nomenclature of the species follows Müller-Motzfeld et al. (2004). Not all specimens of *Bembidion incognitum* and *B. deletum* could be identified to species level and they were thus treated as '*Bembidion incognitum/deletum*' in Table 3.2.

3.3.3 Data analysis

In order to compare species and sites with different numbers of individuals, percentage of total catches per sampling period were used. Total number of species per sampling period and mean number of species per site and sampling period were compared.

For comparison of phenology at different altitudes, the sites were divided into three altitude classes (<1600, 1600-1850, >1850 m a. s. l.) which contained similar numbers of sites. The weighted mean phenological appearance was calculated for every species in each altitude class. Differences among classes were tested with a t-test, whereby we only used data for species which occurred at each sampling site and for which at least 10 individuals per class were found. Differences in phenological appearance in the traits: 'hindwing development' and 'body length' were also tested. For 'hindwing length' the groups 'brachypter', 'dimorphic' and 'macropterous' were tested using a t-test; for body size, species were grouped into 7 classes (mean body length < 3 mm, 3-6 mm, 6-9 mm, 9-12.5 mm, 12.5-20 mm, 20-27 mm, >27 mm) and a Spearman rank correlation was performed. Bonferroni corrections were conducted for each test family. For t-tests, data were checked for normality with Shapiro-tests.

Species accumulation curves (also called sample-based rarefaction curves) are used to compare sampling effort and species richness measures (Buddle et al. 2005; Duelli et al. 1999; Gotelli and Colwell 2001; Ugland et al. 2003). Rarefaction curves for the whole dataset and for each unique sampling period were calculated using Kobayashi's formula (Kobayashi 1974) in the R package 'vegan' (Oksanen et al. 2008; R Development Core Team 2008).

Several reduced datasets with data from two sampling periods were produced. Rarefaction curves and species number per site were compared across the whole dataset, single sampling periods and different combinations of sampling periods.

To understand how the assemblage of carabid beetle species could be represented in the case of reduced sampling effort we computed a dissimilarity matrix based on Bray-Curtis distances. For this analysis, species numbers were standardised to percentage-data of total species numbers per site and square-root-transformed. Based on this matrix a hierarchical cluster procedure was conducted using Ward's minimum variance method.

3.4 Results

In total, 13,585 specimens representing 47 species of carabid beetles were trapped over the sampling period (Table 3.2). The 10 most abundant species occurred throughout the whole altitudinal range of the study area.

General seasonal activity began with a maximum at the beginning of the study and showed a continuously decreasing tendency up until the end of September (Fig. 3.1). Focusing on individual numbers, the highest activity was in June, where >50% of individuals were caught. In July, activity declined slowly, and in the second half of the sampling timespan, August and September combined, only 20% of the total number of individuals were trapped.

The number of recorded species follows a similar trend: after a minute increase up to the first half of July, the number of species decreased. Mean species number per site was almost constant from June to the beginning of July, and then decreased up to the end of the study period (Fig. 3.2 a).

The extremes in beetle activity were greatest at sites above 1850 m a.s.l. relative to the other two altitude classes: the maximum in June was higher and the low activity from the second half of July until September was even more pronounced (Fig. 3.2 b). Differences between the activity phenology of low and mid-altitude classes are not significant ($t=-0.322$, $p=0.753$); however, mean activity of ground beetle species occurring at all elevations is earlier at higher altitudes than at the mid-altitude and lower sites ($t=4.33$, $p=0.001$).

All species of which at least 10 individuals were caught had their activity peak in June or July, approximately two thirds of the species in June, and one third in July (Table 3.2).

Table 3.2. List of carabids trapped over the whole sampling time and their traits ‘hindwing development’ (b: brachypter, d: dimorphic, m: macropteris) and body size class. For each species the sum of individual caught (sum) as well as the percentage of individuals per sampling period 1 to 8 are given.

Species	wing- type	body- size	sum	1	2	3	4	5	6	7	8
				(5.6.- 18.6.)	(19.6.- 3.7.)	(4.7.- 18.7.)	(19.7.- 1.8.)	(2.8.- 15.8.)	(16.8.- 29.8.)	(30.8.- 12.9.)	(13.9.- 26.9.)
<i>Pterostichus jurinei</i> (Panzer, 1803)	b	4	4431	30.1	33.2	16.1	7.3	2.7	1.9	4.7	4.0
<i>Pterostichus burmeisteri</i> Heer, 1838	b	5	2094	25.2	13.4	12.1	9.5	4.5	5.5	17.7	12.0
<i>Pterostichus unctulatus</i> (Duftschmid, 1812)	b	3	1386	24.4	21.2	17.0	11.8	5.3	8.0	9.2	3.2
<i>Pterostichus pumilio</i> (Dejean, 1828)	b	2	1044	20.3	15.8	23.7	23.6	8.7	2.6	2.7	2.7
<i>Pterostichus multipunctatus</i> (Dejean, 1828)	b	4	669	37.1	35.1	4.5	5.8	4.3	3.9	6.1	3.1
<i>Pterostichus melanarius</i> (Illiger, 1798)	d	5	578	13.5	31.1	30.3	11.8	5.4	3.1	4.0	0.9
<i>Abax parallelepipedus</i> (Piller & Mitterpacher, 1783)	b	5	577	9.5	25.1	16.8	19.6	7.3	10.1	10.6	1.0
<i>Trechus obtusus</i> Erichson, 1837	d	2	509	14.3	14.5	20.8	27.3	9.4	5.7	3.9	3.9
<i>Carabus auronitens</i> Fabricius, 1792	b	6	432	19.9	29.9	24.5	16.4	4.4	3.7	1.2	
<i>Carabus violaceus</i> Linné, 1758	b	7	365	5.5	21.9	27.4	29.0	6.8	6.6	2.5	0.3
<i>Amara erratica</i> (Duftschmid, 1812)	m	3	282	31.6	52.8	13.5	1.4	0.7			
<i>Leistus nitidus</i> (Duftschmid, 1812)	d	3	167	10.2	26.3	24.6	16.8	5.4	6.6	9.0	1.2
<i>Oreonebria picea</i> (Dejean, 1826)	b	4	159	32.7	30.8	16.4	15.1	2.5	1.9	0.6	
<i>Calathus melanocephalus</i> (Linné, 1758)	d	3	102	5.9	2.9	28.4	17.6	26.5	12.7	4.9	1.0
<i>Pterostichus strenuus</i> (Panzer, 1796)	d	3	97	52.6	23.7	11.3	6.2		2.1	1.0	3.1
<i>Calathus micropterus</i> (Duftschmid, 1812)	b	3	76	14.5	23.7	28.9	14.5	3.9		11.8	2.6
<i>Harpalus latus</i> (Linné, 1758)	m	4	74	10.8	20.3	12.2	21.6	16.2	12.2	6.8	
<i>Poecilus versicolor</i> (Sturm, 1824)	m	4	73	26.0	52.1	12.3	4.1	4.1		1.4	
<i>Pterostichus diligens</i> (Sturm, 1824)	d	2	73	57.5	20.5	11.0	4.1			2.7	4.1
<i>Dyschirius globosus</i> (Herbst, 1784)	d	1	51	54.9	7.8	15.7	13.7	3.9	2.0		2.0
<i>Cicindela campestris</i> Linné, 1758	m	4	44	15.9	22.7	27.3	13.6	11.4	2.3	4.5	2.3
<i>Carabus sylvestris</i> Panzer, 1796	b	6	36		58.3	16.7	2.8	8.3	2.8	8.3	2.8
<i>Amara aulica</i> (Panzer, 1797)	m	5	32		6.3	50.0	43.8				
<i>Bembidion bipunctatum nivale</i> Heer, 1837	m	2	32	84.4	3.1	9.4				3.1	
<i>Trichotichnus laevicollis</i> (Duftschmid, 1812)	d	3	30	26.7	23.3	13.3	23.3	3.3	6.7	3.3	
<i>Amara lunicollis</i> Schiödte, 1837	m	3	24	29.2	62.5	4.2	4.2				
<i>Notiophilus biguttatus</i> (Fabricius, 1779)	d	2	23	8.7	17.4	17.4	30.4	4.3	4.3	13.0	4.3
<i>Bembidion incognitum/deletum</i>	m	2	19	52.6	21.1	15.8		10.5			
<i>Cychrus attenuatus</i> (Fabricius, 1792)	b	5	19	5.3	5.3	15.8	36.8		5.3	21.1	10.5
<i>Amara nigricornis</i> C.G. Thomson, 1857	m	3	17	17.6	41.2	17.6	17.6			5.9	
<i>Nebria rufescens</i> (Stroem, 1768)	m	4	17	23.5	23.5	23.5	11.8	11.8		5.9	
<i>Bembidion lampros</i> (Herbst, 1784)	d	2	15	73.3	6.7	13.3					6.7
<i>Cychrus caraboides</i> (Linné, 1758)	b	5	11	27.3	45.5	9.1		9.1	9.1		
<i>Bembidion properans</i> (Stephens, 1828)	d	2	7	14.3	57.1	28.6					
<i>Loricera pilicornis</i> (Fabricius, 1775)	m	3	6	16.7	66.7	16.7					
<i>Nebria brevicollis</i> (Fabricius, 1792)	m	4	3	33.3		33.3	33.3				
<i>Agonum sexpunctatum</i> (Linné, 1758)	m	3	2			100.0					
<i>Acupalpus flavicollis</i> (Sturm, 1825)	m	2	1		100.0						
<i>Amara familiaris</i> (Duftschmid, 1812)	m	3	1			100.0					
<i>Amara praetermissa</i> (C.R. Sahlberg, 1827)	m	3	1					100.0			
<i>Carabus glabratus</i> Paykull, 1790	b	7	1			100.0					
<i>Chlaenius nigricornis</i> (Fabricius, 1787)	m	4	1	100.0							
<i>Cicindela sylvicola</i> Dejean, 1822	m	5	1			100.0					
<i>Harpalus affinis</i> (Schränk, 1781)	m	4	1						100.0		
<i>Pterostichus vernalis</i> (Panzer, 1796)	d	3	1			100.0					
<i>Synuchus vivalis</i> (Illiger, 1798)	d	3	1					100.0			
Total			13585	24.9	25.8	17.2	12.1	4.8	4.1	7.0	4.2

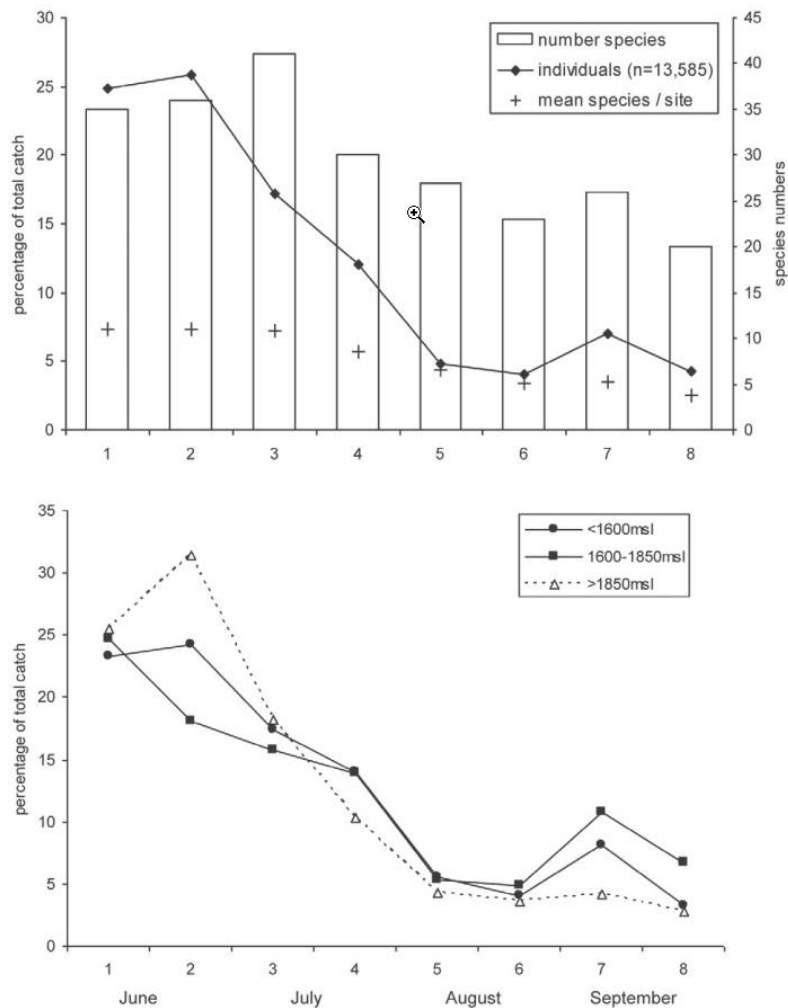


Figure 3.2: Phenology of ground beetles. Fig. 3.2 a: Overview over all sites. Number of individuals is converted to percentage of total catch. Fig. 3.2 b: Separated for the three site classes of altitude. On the horizontal axis the sampling interval is given. For exact sampling period see caption of Table 3.2.

Species can be divided into three groups according to their phenology: (1) The first and largest group of species shows quite a distinct activity peak in June (Fig. 3.3 a) and often a strong decline already occurring in July (e.g. *P. multipunctatus*, *B. bipunctatum*). Some of these species are almost absent in the second half of the year (*A. erratica*, *B. bipunctatum*). The strength of the spring activity peak may also be less pronounced (e.g. *C. auronitens*). (2) A second group of species shows a delayed activity peak (Fig. 3.3 b). In most cases, the magnitude of the peak was weaker than seen in the early species. In species with a delayed activity peak, there are also cases with absence in the second half of the year (*A. aulica*). (3) The third group is comprised of species that show no clear activity peak (Fig. 3.3 c), i.e. which are active over the entire sampling timespan. Only a few species fit into this latter scheme. Most of these are characterized by a weak peak in June, followed

by a slow decline in activity. Some of the species exhibit a relatively high activity in autumn (*P. burmeisteri*, *A. parallelepipedus*).

We were unable to find any significant relationship between phenological appearance and hindwing development of the species. Similarly, for body size no significant difference was found, although there is a weak trend of larger species appearing later in the year ($t=1.61$, $df=44$, $p=0.114$).

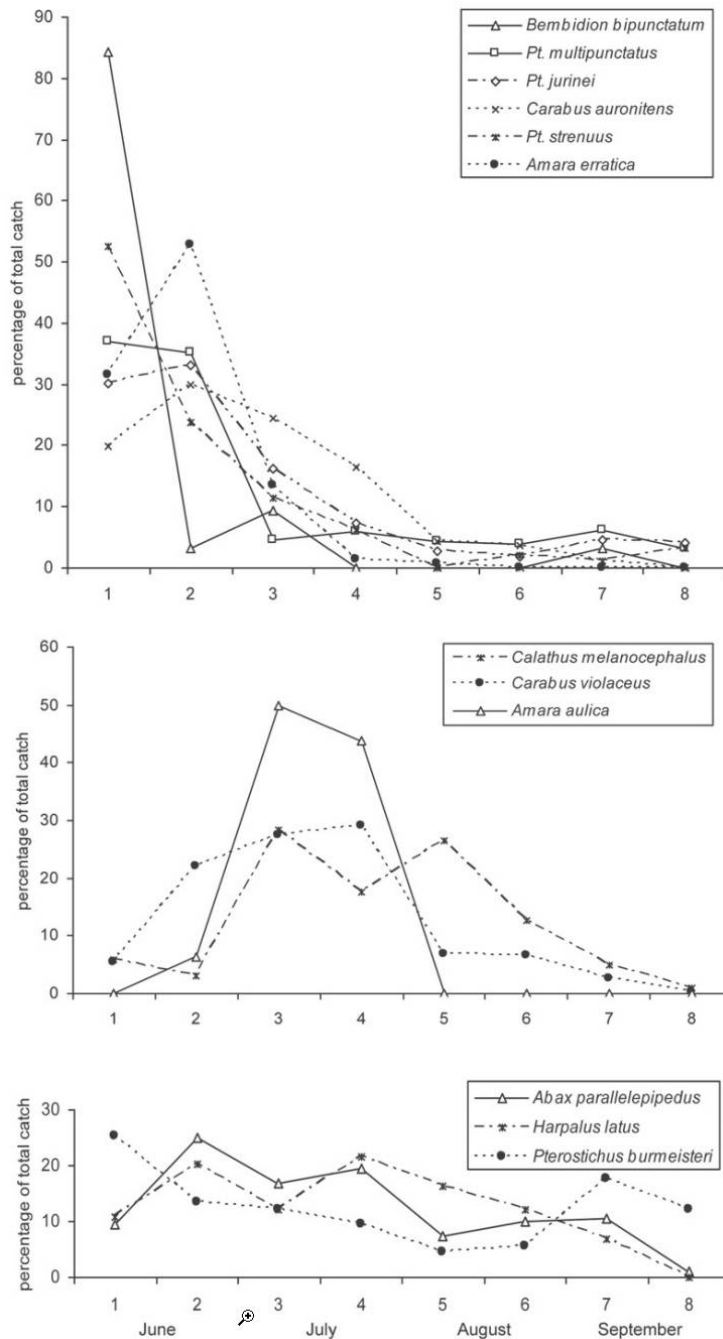


Figure 3.3: Phenology of single species. Fig. 3.3 a: Species with an early activity peak, Fig. 3.3 b: Species with a delayed activity peak and Fig. 3.3 c: Species without clear activity peak. On the horizontal axis the sampling interval is given. For exact sampling period see caption of Table 3.2.

The sample-based accumulation curves of the first three sampling periods are almost identical at the start, and considerably steeper than the curves of subsequent periods and the curve based on the entire dataset (Fig. 3.4). After 25 samples, the curves of the first three periods split: the third period curve attains higher values, and the first and second period curves follow a similar trend.

Decreasing overall activity after the spring peak is also discernible in the rarefaction curves: the curves for sampling periods 4-8 are clearly below the curve for complete sampling (the curve for sampling period 4 is greater than the total sample curve at the start of the rarefaction process and then falls below it).

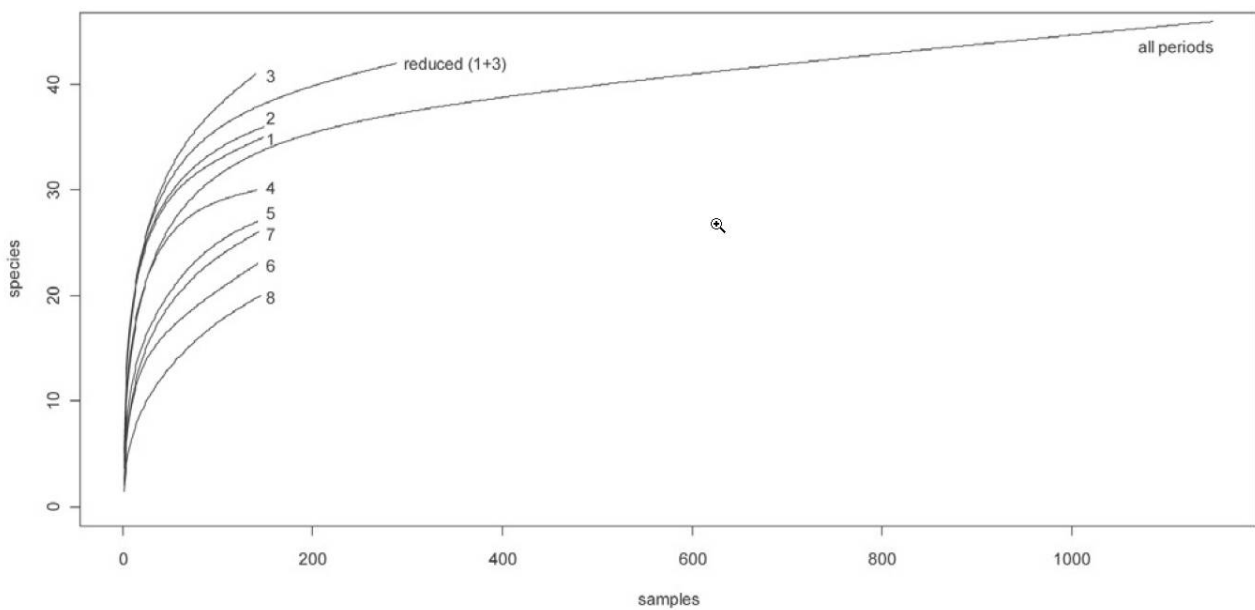


Figure 3.4. Sample-based rarefaction curves. Numbers refer to the number of sampling period.

Table 3.3 illustrates the effect of a reduced sampling effort on observed species richness. While single sampling periods achieve a maximum of 65% of the total number of species over the entire sampling timespan, a combination of two early sampling periods can exceed 80% of the total amount of species (sampling periods 1 and 2 or 1 and 3). Best results are obtained when sampling effort is reduced to sampling periods 1 and 3. With the reduced datasets for sampling periods 1 and 3, 91.3% of all species were detected. Per site, the mean quota was 83%, and varied between 68.8 and 100%. The quota of species detected was seen to be independent of altitude or number of specimens caught.

Table 3.3. Comparison of species trapped per site for different sampling efforts. In the column species the total number of species per site is given. Percentage of species caught is indicated for each single sampling period and a selection of two combined periods. The mean percentage of species caught per site (mean/site) for each effort is calculated.

site	single periods								two periods				species
	1 (5.6.-18.6.)	2 (19.6.-3.7.)	3 (4.7.-18.7.)	4 (19.7.-1.8.)	5 (2.8.-15.8.)	6 (16.8.-29.8.)	7 (30.8.-12.9.)	8 (13.9.-26.9.)	1+2	1+3	2+3	1+4	
V02	64	59	73	41	23	23	32	14	86	86	82	73	22
V03	68	64	73	32	36	32	32	27	86	86	82	73	22
V05	76	76	57	57	19	14	19	10	90	86	90	81	21
V06	56	75	50	38	56	44	38	6	81	69	75	63	16
V08	77	54	69	62	62	62	31	15	77	92	77	77	13
V10	45	65	80	60	45	40	25	20	65	85	95	65	20
V11	63	69	69	50	44	13	31	25	81	88	81	75	16
V16	71	53	47	29	41	29	18	12	71	88	71	76	17
V23	53	100	60	67	47	27	33	7	100	73	100	80	15
X01	82	88	71	47	24	12	18	24	94	88	94	82	17
X03	64	57	71	43	50	36	36	29	86	86	86	64	14
X04	61	56	50	44	44	44	33	28	72	72	67	72	18
X05	73	68	77	64	45	36	36	32	95	100	82	91	22
X07	53	53	60	73	60	40	20	27	67	73	67	80	15
X08	73	60	60	60	47	47	47	27	87	87	73	80	15
X09	83	67	67	67	50	33	33	25	92	83	83	100	12
X10	46	92	77	38	46	38	23	15	92	85	100	54	13
X11	63	53	63	42	37	37	32	32	68	79	68	68	19
X13	65	59	65	47	18	18	53	35	71	88	82	76	17
X14	53	73	67	53	33	47	47	33	87	80	80	60	15
X15	71	57	71	93	50	43	57	29	79	86	71	93	14
X17	79	43	50	43	36	14	21	21	79	79	50	86	14
X18	53	37	58	32	21	11	26	11	63	79	63	63	19
X20	63	69	44	56	44	25	19	44	81	69	88	69	16
X21	68	73	68	50	27	18	27	14	82	86	86	73	22
all sites	76	78	89	65	59	50	57	43	83	91	91	80	46
mean/site	65.4	65.3	64.8	52	40.9	32	32.4	23.2	81.3	82.9	79.7	75	10

Classification showed that a reduced dataset (periods 1 and 3 only) represents the assemblage structure in a similar way to the complete dataset: All sites are grouped together until the last splitting, where they are divided as a result of sampling intensity (Fig. 3.5).

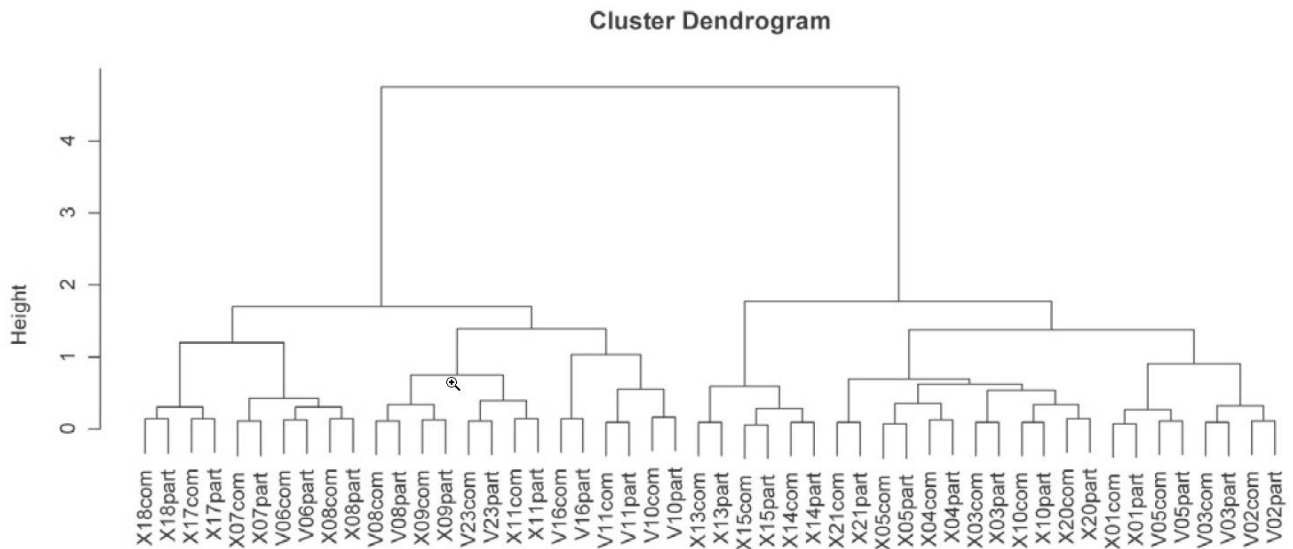


Figure 3.5. Dendrogram of sites with data from complete sampling (comp) and sampling periods 1 and 3 (part). The dendrogram is based on Bray-Curtis distances and uses Ward's minimum variance method.

3.5 Discussion

The strong activity peak observed in our study at the start of the plant growing season has already been observed in many carabids in mountain regions, especially in subalpine and alpine ecosystems (Brandmayr et al. 2003b; De Zordo 1979a; b; Gereben 1995; Janetschek, Meyer, Schatz and Schatz-de Zordo 1987; Lang 1975; Löffler and Finch 2005; Ottesen 1996; Refseth 1984; Sharova and Khobrakova 2005). While depending on altitude, exposition and longitude, the weeks immediately after snow-melt are characterised by an activity peak in many species. The shortened plant growing season and the time in which the larvae are able to develop are given as an explanation for this. A fast start to reproduction in cool ecosystems is advantageous, as larval development takes longer under such conditions (cf. Ferenz 1975; Paarmann 1966). Food availability is another possible explanation; many swarming or flying insects (especially Diptera and Hymenoptera) are attracted to the white snow fields. After landing on these fields the insects are immobilised by the low temperatures. In most cases, ground beetles can pick them up live overnight or, later, as carcasses on snow fields after snowmelt. In these cases, some authors use the term "snow edge species", i.e. species which are adapted to cold and humid conditions and disappear very rapidly after snowmelt (Brandmayr et al. 2005; Franz 1970; Holdhaus 1954; Marggi 1992).

However, snow edge species (Marggi 1992), such as *Bembidion bipunctatum nivale*, are not the only species most often trapped after snow melt. Species with broader habitat preferences show

increased activity during that time. Prevailing conditions after snow melt (open structure of vegetation and low “Raumwiderstand” sensu Heydemann 1956, the resistance of vegetation structure to the locomotory movement of a given species, high temperatures during sunshine combined with a high soil humidity) might be advantageous for several species.

While most papers focus on the abundant species, our data show that an early activity peak can also be observed for the less abundant species. Ottesen (1996) made the same observation for carabids in alpine sites in Norway. However, this was not true for other groups of epigeic arthropods, as he observed an autumn activity peak for some species of staphylinids.

Although high spring activity was seen for all species, we observed differences between species: we were able to divide our species into three groups according to their phenological appearance. While the first group (early and strong spring activity peak) is most frequently described in mountain ecosystems, delayed spring activity has already been shown for some species by other authors (De Zordo 1979b; Refseth 1984), and a species without a strong activity peak was presented (Sharova and Khobrakova 2005). Our data does not give a clear indication of the reasons for the observed phenological differences among species, at least there were no simple relationships between the traits we tested.

The observed activity densities of species, with some species having a strong and early peak and others with a delayed peak led us to the conclusion that the best results can be expected by reducing the sampling to two periods at the beginning of the season. In fact, sampling periods 1 and 3 showed the highest average coverage of the sites’ species richness, and the quota of species trapped was better than that suggested by Duelli et al. (1999) for the so-called standard minimum programme for lower altitudes (Duelli et al. 1999). This means that for high altitudes our suggestion to reduce the sampling effort results in a more robust data set than similar approaches for lower altitudes, as the beetles’ activity seems to be more concentrated within a shorter period in mountain ecosystems. The phenological data of other analyses conducted in different habitats from the upper montane zone upwards supports an approach that focuses on an early first sampling period and a delayed second (De Zordo 1979a; b; Gereben 1995; Janetschek, Meyer, Schatz and Schatz-de Zordo 1987; Lang 1975; Löffler and Finch 2005; Ottesen 1996; Refseth 1984; Sharova and Khobrakova 2005). Results of the classification procedure showed that with our reduction in sampling effort, community structure is represented well. A reasonably reduced sampling effort improves the chances of including carabid beetles in monitoring programmes in mountain areas, e.g. to evaluate the conservation status of habitats in Natura 2000 areas. If a reduction in sampling effort is inevitable, we recommend that the minimum sampling effort for carabids in mountain ecosystems

should be two fortnightly sampling periods, the first immediately after snow melt and a second after a break of two weeks.

3.6 Acknowledgements

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4 Beitrag 2: Protected habitats of Natura 2000 do not coincide with important diversity hotspots of arthropods in mountain grasslands

publizierter Artikel

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4.1 Abstract

1. Biodiversity assessments for conservation planning are often restricted to a limited set of species. This is also the case in the context of Natura 2000, where surveys focus strongly on vegetation and selected vertebrate species. Without cross-taxon congruence, however, this approach does not guarantee that the relevant aspects of biodiversity are appropriately represented.

2. We here assess the diversity of vascular plants, carabid beetles and spiders in mountain grasslands of the European Alps. We address the questions if there are distinct species assemblages in different habitats and if these assemblages show sufficient cross-taxon-congruence. Furthermore, we test if habitats that are protected based on vegetation characteristics also inhabit an arthropod fauna with highest conservation value.

3. We found only weak agreement in assemblage composition and no positive correlation in species richness across the three focal taxa. Furthermore, we found a negative correlation between species richness of plants and carabids, indicating opposing taxon-specific responses to habitat differences and land use intensity. Species richness was higher at protected sites for plants, but not for carabids and spiders. This applied also to the subset of species with highest conservation value.

4. Our results show that prioritisation of sites for conservation based solely on vegetational aspects does not necessarily coincide with important sites for arthropods. This calls for a multi-taxon approach in conservation planning to cover more of the endangered and range-restricted species. Species- and surrogate-based conservation efforts, like the Natura 2000 directive, should therefore be extended to embrace the diversity of arthropods.

4.2 Introduction

The world is facing a global loss of biodiversity that is also of societal concern calling for measures to prevent biodiversity loss (Butchard *et al.* 2010). As resources for nature conservation are limited, prioritization is crucial to maximise conservation efficiency (Myers *et al.* 2000; Davies & Cadotte 2011). Biodiversity assessments play a major role in conservation planning, to identify areas for conservation, to develop conservation strategies and to evaluate conservation actions (Gaston 1996; Meine 2018). Such assessments are hampered by constraints of funds and time, spatial and temporal complexity, but sometimes also by lack of taxonomic expertise (Gaston 1996; Sauberer *et al.* 2004;

Gioria *et al.* 2011). Efforts can possibly be minimised by the use taxonomic surrogates that represent a larger range of biodiversity (Gardner *et al.* 2008). Taxon surrogacy is based on the assumption of correlated species richness and concordance in assemblage composition across different taxonomic groups (Noss 1990; Prendergast *et al.* 1993; Santi *et al.* 2010).

Since surrogates can potentially work as efficient biodiversity indicators, the use of surrogates in biodiversity assessments is hotly debated (e.g. Cabeza *et al.* 2008, Lewandowski *et al.* 2010; Barton *et al.* 2014; de Morais *et al.* 2018). One major criticism is that cross-taxon congruence is often low so that the required representation is not guaranteed (Favreau *et al.* 2006; de Morais *et al.* 2018). Hence, many authors promote multi-taxon approaches (Kotze & Samways 1999; Finch & Löffler 2010), while others aim to specify the conditions that justify the use of surrogates (Favreau *et al.* 2006; Westgate *et al.* 2014). The latter includes the question which specific taxa work best as general surrogates or as surrogates for specific other taxa. Vascular plants are often discussed as possible general surrogates, since the group is taxonomically rich and ecologically well described, including a number of specialist species (Prendergast *et al.* 1993; Saetersdal *et al.* 2004; Su *et al.* 2004). Furthermore, vascular plants are comparably easy to be identified in the field, they are persistent at least during the vegetation period and as primary producers they structure the habitat for consumers (Anand *et al.* 2005; Vera *et al.* 2008; Santi *et al.* 2010). However, how far plants can replace surveys of other taxa, in particular those that are more cryptic and taxonomically challenging, is not always clear (Santi *et al.* 2010).

Despite the criticism concerning the use of surrogates for conservation decisions, it is common practice to restrict biodiversity assessments to a few taxonomic groups or even a subset of indicator species (Vellend *et al.* 2008). This is also the case in the context of Natura 2000, one of the largest international networks in conservation and a central element in biodiversity conservation in the European Union (Orlikowska *et al.* 2016). The Annexes of the Nature 2000 Directive play a direct role in guiding conservation planning and decision making in the European context, as they list the protected species (Annexes 2 and 4) and the protected habitats (Annex 1), which form the basis for defining the “Special Areas of Conservation” (Hochkirch *et al.* 2013). These Annexes list mostly rare, endemic or endangered species that themselves are of conservation concern, but they may be of limited value to general biodiversity conservation (see Cardoso 2012; Rosso *et al.* 2018 for a discussion of limitations and critiques about current species selection).

Invertebrates are significantly underrepresented in Annexes 2 and 4 of the Natura 2000 Directive. Among the about thousand species listed, there are only 122 arthropods (including only 38 species of beetles and a single spider species, Cardoso 2012), although insects and other invertebrates represent a major portion of total animal biodiversity. Arthropods are ecologically relevant as pollinators, pest control agents and as primary and secondary consumers they play a significant role in food webs (Klein *et al.* 2007, Schuldt & Assmann 2010, Hallmann *et al.* 2017). This diversity is currently at a significant decline, which has recently been convincingly demonstrated for the abundance of flying insects in Central Europe (Hallmann *et al.* 2017, 2018). The characterisation of habitats as listed in Annex 1 is mainly based on vegetation. Animals are rarely referred to in the characterisation of habitats, and most animals mentioned in the habitat descriptions are vertebrates in aquatic ecosystems (EC 2013). Despite the focus on vascular plants and vertebrate species in the context of Natura 2000, it is not known whether these taxa may efficiently identify areas which are important for invertebrate species (Wolters *et al.* 2006, Lewandowski *et al.* 2010, Schuldt & Assmann 2010, Westgate *et al.* 2014).

We here assess the diversity, assemblage composition and cross-taxon congruence of vascular plants, carabid beetles and spiders in mountain grasslands of the European Alps in southern Germany. The Alps represent a biodiversity hotspot in Europe and host a large number of endemic species (Tribtsch 2004; Rabitsch 2009). The Alps have undergone substantial climatic and land use changes over the last decades. This has led to substantial changes in habitats, in particular a decline of grasslands with low land use intensity (Streifeneder & Ruffini 2007; Marini *et al.* 2009). Alpine grasslands are particularly rich in endemic species, specifically among groups with low dispersal ability, such as many insects. Climate change and land use change may challenge their persistence. Our study was conducted within the frame of an applied conservation project that aimed to assess and evaluate different sites with regard to management in the future.

We used the survey of vascular plants, carabid beetles and spiders to assess cross-taxon patterns of biodiversity. Carabid beetles and spider represent two less often studied groups of arthropods that are not well represented in species- and surrogate-based conservation efforts such as the Natura 2000 directive. We address three specific questions. (1) Do the three groups show similar assemblage composition when compared across different habitats? (2) Does local species richness correlate across the three groups, such that species richness in one group is predictive for species richness in other groups? We analyse this separately for total species richness and richness of species of conservation concern. (3) Do protected habitats that were identified based on vegetation

characteristics also inhabit the most valuable arthropod fauna? Answers to these questions have implications for the use of surrogates in conservation practise.

4.3 Materials and methods

4.3.1 Study area

We studied species diversity of vascular plants, carabid beetles and spiders of the mountain pasture “Alpe Einödsberg“ in the German part of the Alps (47.32°N; 10.28°E). The study area represents a part of the “Allgäuer Hochalpen“, a territory listed as Special Area of Conservation in the European conservation system Natura 2000. The study area ranged in altitude between 1,400 to 2,000 meters above sea level and encompassed pastures with a total area of about 120 ha (Höfer *et al.* 2010). Most of the predominantly west-facing slopes consist of meadows dominated by matgrass (*Nardus stricta*). Woodland belts of Norway spruce (*Picea abies*) and krummholz formed by green alder (*Alnus viridis*) occur throughout the pasture zone. There is a ridge of 2 km length running north-south along the upper section of the pasture.

The pasture has been intensely grazed by sheep during most of the 20th century (up to 15 sheep per hectare). However, the grazing regime changed markedly in 2001. Most parts were from thereon grazed at low intensity by cattle and in some places grazing was completely abandoned. Grazing intensity was highly heterogeneous mainly for topographic reasons. The steep parts of the pasture were grazed at low intensity. Grazing intensity, especially at the time of sheep keeping, was highest on the ridge that was preferably used by resting livestock. Deposition of faeces has been especially high at those places, so that vegetation on the ridge differed clearly from the surrounding grasslands. For comparison we also sampled four ungrazed ridges in other parts of the “Allgäuer Hochalpen“. In total we sampled 26 plots (Table 1.1) that were assigned to four habitat types: montane grassland (5 plots), subalpine *Nardus*-grassland (9 plots), grazed ridges within the study area (6 plots) and ungrazed ridges outside the main study area (3 plots). Three plots could not be assigned to any of those habitat types.

Plots were classified as protected/unprotected according to data on protected habitat types (in this case habitat type 6150 Siliceous alpine and boreal grasslands with the corresponding vegetation) from the Natura 2000 Management Plan of this Special Area of Conservation, which is currently in preparation (RvS 2013). In a few cases we deviated from the classification in the management plan, since resolution was rather coarse on the local scale. In these cases we used a more detailed map of vegetation types to identify habitat type 6150 (Urban & Hanak 2010).

4.3.2 *Arthropod sampling*

Arthropods were sampled using pitfall traps: plastic cups of 6 cm in diameter, filled with 5% acetic acid, 95% water and a drop of detergent to reduce surface-tension, protected against damage by cattle and rain by a metal construction holding a transparent plastic cover (see Fig 1a in Höfer *et al.* 2010). Traps were installed in two rows of three traps with a distance of 6 m from each other, resulting in a rectangular area of 6 x 12 m. Catches from all six pitfall traps at each plot were pooled in the analyses.

Pitfall traps were opened for two weeks in June (just after the first snow melt at the ridge) and in early July. This sampling scheme was shown to be adequate for carabid beetles in these mountain habitats (Harry *et al.* 2011). All plots were sampled in the context of a conservation project between 2003 to 2008. The complete sampling scheme is described in Höfer *et al.* (2010). For our analysis, arthropod samples were taken from 2008 (16 plots), in 2007 (4 plots), 2005 (3 plots) and 2004 (3 plots). Carabids were identified to species level using Müller-Motzfeld *et al.* (2004) by I. Harry. Spiders were identified using Heimer & Nentwig (1991), Nentwig *et al.* (2003) and Roberts (1993) by T. Blick, H. Höfer, F. Meyer and C. Muster. Vouchers were deposited at the State Museum of Natural History Karlsruhe. Species nomenclature follows Löbl & Löbl (2015) and World Spider Catalog (2019).

4.3.3 *Vegetation surveys*

Vegetation survey data were taken from Urban & Hanak (2010) who surveyed the same 26 plots in 2008. All vascular plant species were identified in an area of 5 x 5 m that was centred in the middle of plots used for arthropod sampling. Each species' coverage estimated following the system of Braun-Blanquet (1964). Briefly, the Braun-Blanquet coverage estimates assign each plant species to one of seven cover classes (r = single plants, + = 2-5 plants with coverage <1%, 1 = 6-50 plants with coverage <5%, 2 = more than 50 plants and coverage <5% or coverage 5-25%, 3 = coverage 26-50%, 4 = coverage 51-75%, 5 = coverage 76-100%).

4.3.4 *Quantification of cross-taxon congruence*

Cross-taxon congruence can be assessed as (1) assemblage concordance that is the covariance in assemblage structure across habitats or as (2) the correlation in patterns of species richness and/or diversity (Pearson & Carroll 1999, Gioria *et al.* 2011). Both approaches yield valuable insights. The

first is more ecological, since it focuses on how distinct taxon-specific assemblages are in different habitats and how assemblages of different taxa agree in their habitat-specific distinctiveness. This is relevant for habitat classification. The second focuses on agreement in overall biodiversity patterns and is relevant in particular for conservation applications.

4.3.5 Statistical Analyses

We used ordination by non-metric multi-dimensional scaling (NMDS) on each of the three taxonomic groups for analysing assemblage composition. NMDS is a technique that does not assume multivariate normality and is largely robust to zero values (i.e. shared absences of species). Abundances of carabid beetles and spiders were log-transformed prior to the analysis to avoid that a few highly abundant species dominate the results. Braun-Blanquet plant cover estimates were converted to a scale from 1 to 7 (van der Maarel 2007). We used the Bray-Curtis measure as dissimilarity index in NMDS, which is well suited for species abundance data because it ignores variables that have zeros for both objects (Dytham 1999). NMDS was used to reduce complexity to three dimensions that gave acceptable stress values.

Similarity of species composition between the three taxonomic groups was investigated using Procrustes analyses of NMDS outputs (Gower 1971). Procrustes analysis is a multivariate ordination technique that allows an estimation of the correlation among data matrices using a rotational-fit algorithm by centring, scaling, reflection, rotation and dilation (Jackson 1995). This technique is considered to be more powerful in detecting congruence between two assemblage matrices than Mantel correlations and offers further options for data examination (Peres-Neto & Jackson 2001; Gioria, Bacaro & Feehan 2011; Lisboa *et al.* 2014). We used the Procrustean fit parameter m^2 as a measure of matrix concordance. m^2 is the sum of squared residuals between matrices in their optimal superimposition (Gower 1971). The statistical significance of m^2 for each pair of matrices was assessed using PROTEST (Jackson 1995; Oksanen *et al.* 2018).

The second aspect of cross-taxon congruence is the comparison of species richness across different taxa and plots. We compared total species richness and species richness of a subset of “important species”, i.e. species either registered in the national or regional red list of endangered species and/or representing montane and subalpine grasslands specialists. This information was taken from Blick & Scheidler (2003); Lorenz (2003); GAC (2009); Schmidt *et al.* (2016) and BfN (2017). We estimated correlations of total and important species richness between taxa.

We also tested whether total or important species richness was higher at protected habitats than at non-protected habitats. This comparison was implemented as taxon-specific independent sample *t*-tests.

Statistical analyses were conducted using R 3.2.2 (R Core Team 2015), including the packages *vegan* (Oksanen *et al.* 2018) and *MASS* (Venables *et al.* 2002).

4.4 Results

We collected 4,559 carabids (21-542 per plot) and 9,941 spiders (53-1,048 per plot). We observed 44 species of carabids (8-22 per plot) and 101 species of spiders (9-31 per plot). Vegetation surveys yielded 253 species of vascular plants (11-66 per plot, Table 4.1).

Table 4.1: Summary of species richness and abundance of plants, carabids and spiders at 26 sampling sites. For all three groups mean, standard deviation (SD), minimum (min) and maximum (max) of species richness is given.

	sum individuals				species richness			
	mean	SD	min	max	mean	SD	min	max
all plants	-	-	-	-	34.9	14.3	11	66
important plants	-	-	-	-	12.2	7.0	5	31
all carabids	175	133	21	542	14.1	3.4	8	22
important carabids	131	129	10	472	8.5	2.9	4	14
all spiders	382	255	53	1048	19.0	5.0	9	31
important spiders	95	126	3	418	4.3	1.8	1	10

4.4.1 Ordination of plots

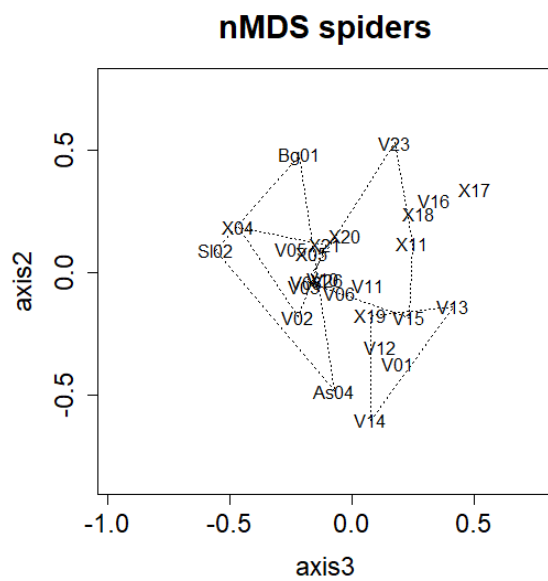
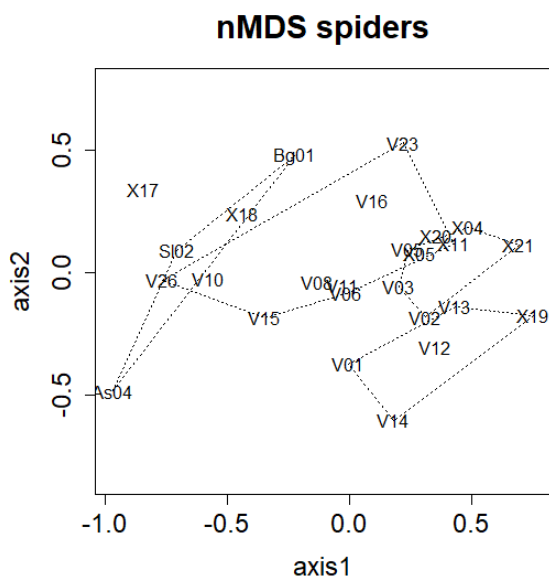
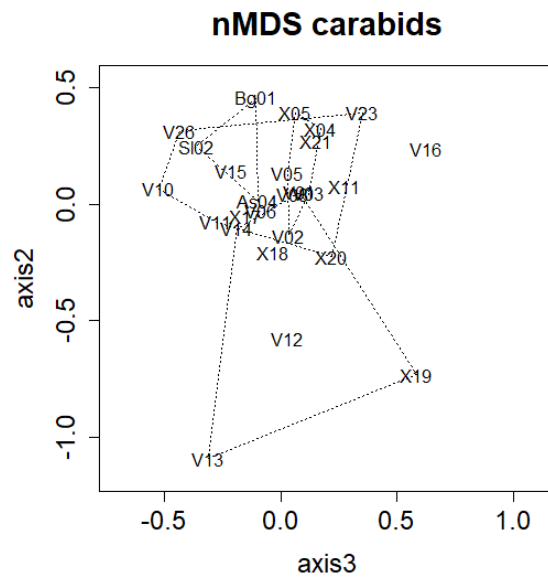
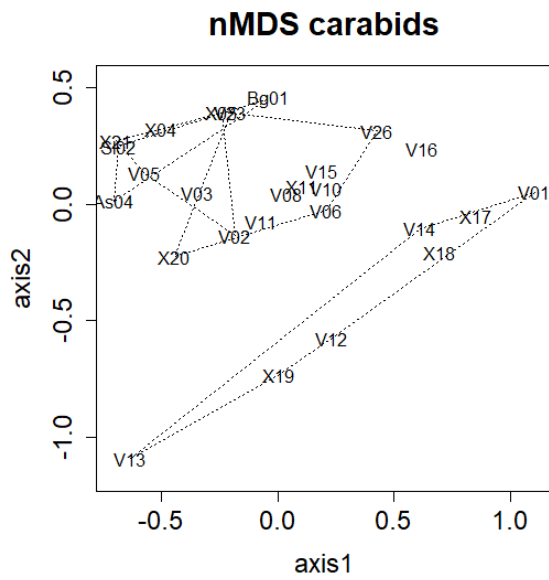
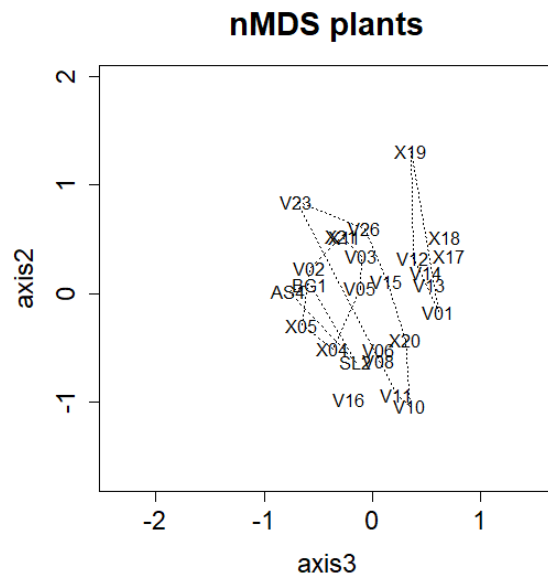
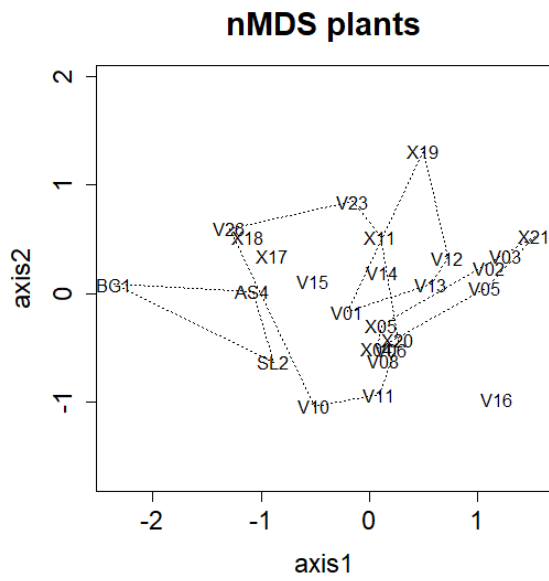
Stress of the NMDS varied between 9 and 10.5 percent for the three groups. Despite some overlap in the first two dimensions, habitat types formed discrete clusters when assessed in three dimensions (Fig. 4.1). The lower montane sites were separated most clearly from higher sites in all three taxonomic groups. In plants and spiders, the grazed and ungrazed ridges were separated clearly along the first axis and the subalpine *Nardus*-grasslands positioned in-between. In carabids, however, plots on grazed and ungrazed ridges formed closely positioned clusters, separated more strongly from the *Nardus*-plots.

Procrustes analyses showed significant pairwise correlations of the ordinations across all three taxa (Table 4.2). Correlation of ordinations between plants and spiders were strongest ($m^2 = 0.64$; $r = 0.60$), followed by carabids/spiders ($m^2 = 0.66$; $r = 0.58$) and plants/carabids ($m^2 = 0.78$; $r = 0.47$).

Table 4.2: Results of Procrustes Analysis of correlations in species composition for every pair of groups tested.

groups	m^2	cor (r)	p
plants spiders	0.64	0.60	0.001
carabids spiders	0.66	0.58	0.001
plants carabids	0.78	0.47	0.004

Figure 4.1 (next page): Results of a three dimensional nMDS for the three groups plants, carabids and spiders. The four habitat types (lower montane grasslands, upper montane Nardus-grasslands, ridges with high grazing intensity, ungrazed ridgeds) are outlined.



4.4.2 Comparison of species richness

In most cases there was no evidence for correlations among taxonomic groups in species richness (Table 4.3, Figure 4.2). The only statistically significant effect was a negative correlation between total species richness in carabids and plants ($r = -0.41$, $p = 0.038$), indicating species richness showed opposing trends in these two groups.

Table 4.3: Results of species richness correlations. We tested the full dataset (all species) as well as a selection of species with high relevance in conservation (important species). Total species richness as well as richness of important species in carabids showed no statistical evidence of deviation from normality (Shapiro-Wilk normality test all $P > 0.11$), while richness of important species in spiders ($P = 0.002$) and plants ($P = 0.036$) did deviate from statistically normality (see Figure 4.2).

	groups	pearson correlation		spearman correlation	
		r	p	rho	p
all species	plants/carabids	-0.41	0.038	-0.43	0.030
	plants/spiders	0.19	0.359	0.16	0.45
	carabids/spiders	0.14	0.50	0.11	0.61
important species	plants/carabids	-0.10	0.614	-0.20	0.33
	plants/spiders	0.24	0.246	0.12	0.57
	carabids/spiders	0.27	0.19	0.22	0.28

Species richness was higher at plots classified as protected habitats in plants (all species and important species), but not for carabids and spiders (Table 4.4). For carabids and spiders we found no differences between plots in protected and unprotected habitats neither in total species richness nor in richness of important species. Linear models showed that the difference between taxa, tested as the interaction between taxon and habitat status, was statistically significant when comparing plants to both arthropods taxa (all species: $F_{2,72} = 9.31$, $P = 0.00025$, important species: $F_{2,72} = 7.55$, $P = 0.0011$), but not between carabids and spiders (all species: $F_{1,48} = 0.08$, $P = 0.78$, important species: $F_{1,48} = 0.35$, $P = 0.56$).

Table 4.4: Results of t-tests for differences of species richness between sites mapped as protected and sites not mapped as protected. Data is given for the full dataset (all species) as well as a selection of species with high relevance in conservation (important species) of all three groups.

	not protected (n=10)	protected (n=16)	T	df	p
all plants	25	41.1	3.36	20.8	0.003
important plants	9.6	19.3	3.48	21.6	0.002
all carabids	14.7	13.7	-0.73	18.8	0.48
important carabids	8.8	8.3	-0.43	14.9	0.67
all spiders	19.2	18.9	-0.15	15.6	0.88
important spiders	4.1	4.4	0.43	22.4	0.67

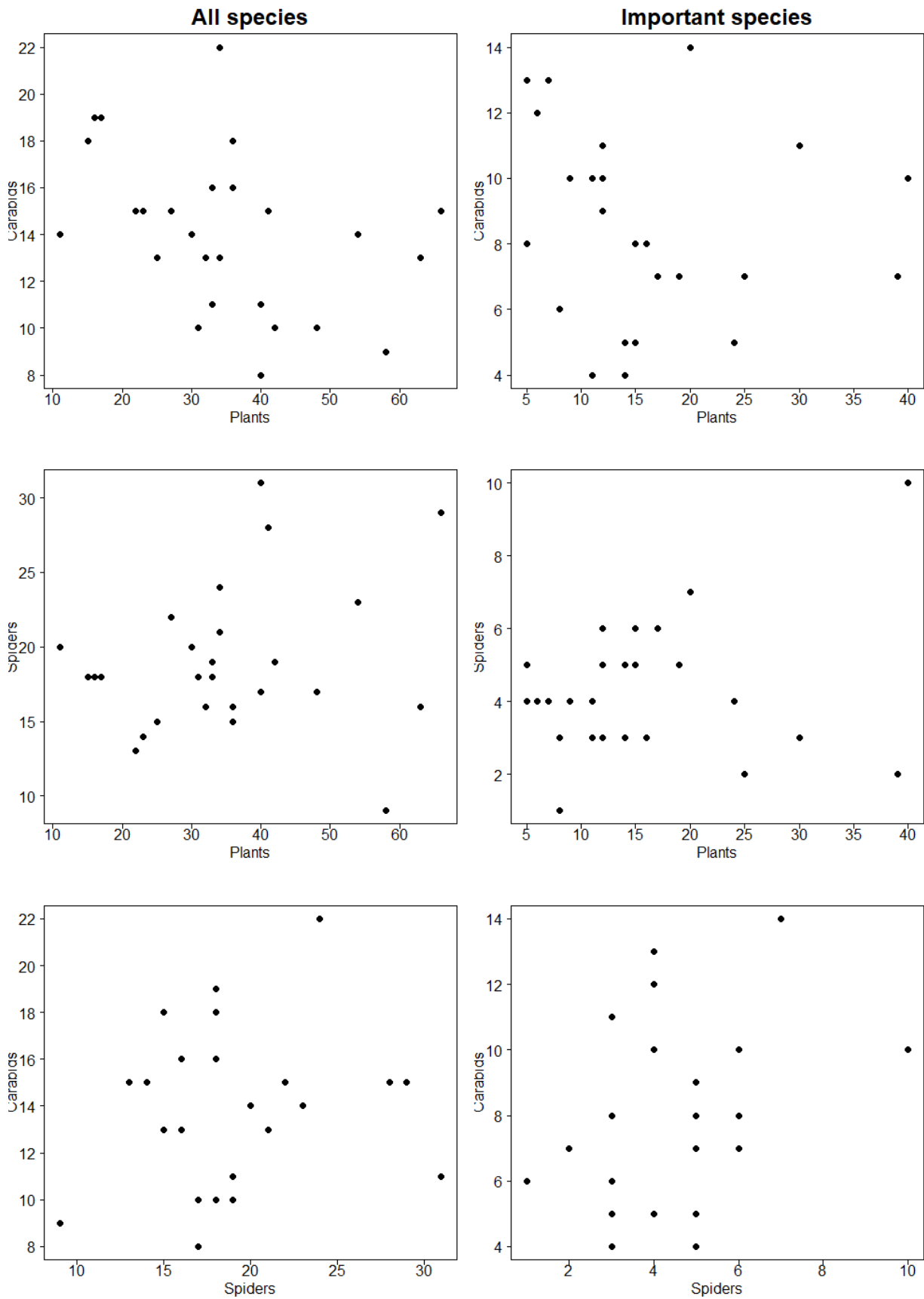


Figure 4.2: Pairwise scatterplots of species richness across plots for the three taxa. The left column shows the total number species, the right column shows the number of important species.

4.5 Discussion

We here report on cross-taxon congruence in assemblage composition and species richness across carabid beetles, spiders and vascular plants in mountain grasslands. High cross-taxon congruence is fundamental for taxon surrogacy and so of high relevance to conservation practice. We found overall similarity in species composition of the plots across the three taxa, but also significant differences, in particular a negative correlation between species richness of plants and carabid beetles, a lack of association between species richness and site's prospective conservation status defined by habitat type (and thus largely by vegetation) and different clustering of habitat-specific assemblages between carabids and the other two taxa. Our results have implications for the use of surrogates in conservation planning in mountain grasslands.

4.5.1 Cross-taxon congruence of species composition

We found significant correlations in species composition between all three taxonomic groups, indicating that patterns of ordinations of the three groups show some similarities. Interestingly, the two functionally more similar groups of epigeic arthropods did not show the strongest correlation. A stronger correlation was found between plants and spiders. Previous studies in montane grasslands have found that carabids assemblages are more strongly influenced by soil parameters, while spiders are primarily influenced by vegetation structure (Luff and Rushton 1989). Differences in soil properties and vegetation structure are pronounced in our study area, especially between sites on the ridge and on slopes. This dependency on different habitat features (soil, vegetation) might explain the differences between the two arthropod groups. Thus, functional similarity does not imply high cross-taxon congruence in species composition (see also Lovell *et al.* 2007).

Although we found significant correlations of species assemblages in all cases, strength of these correlations was overall weak. Heino (2010) suggests that concordance between multiple organism groups is weak if m^2 -values > 0.5 . Heino (2010) points out that significant congruence is likely to emerge in analyses where significance testing is based on randomisation tests, which may lead to highly significant results even if the strength of correlations is very low. Consequently, significant congruence is more often reported for species composition than for species richness (Gioria *et al.* 2014). Our results are similar to other studies in grassland ecosystems, where species composition did show no or just few strong correlations and often showed high variability among taxa (Niemela & Baur 1998; Oertli *et al.* 2005, Lovell *et al.* 2007; compare also Westgate *et al.* 2014).

4.5.2 Cross-taxon congruence of species richness

We found no significant positive correlations in species richness across the three taxa, and correlation coefficients were generally low. This is in agreement with most other studies in grassland ecosystems, where no or at least no strong correlations were found (Niemela & Baur 1998; Vessby *et al.* 2002; Su *et al.* 2004; Oertli *et al.* 2005; Marini *et al.* 2009; Koch *et al.* 2013). However, strong correlations are required when some taxonomic groups are used as surrogates in conservation planning, as only strong correlations lead to mutual informativeness across taxonomic groups. Threshold values of $r = 0.7$ (Heino 2010) or $r = 0.75$ (Lovell *et al.* 2007) have been proposed. Such strong correlations were rarely observed in grassland ecosystems. Sauberer *et al.* (2004) observed strong correlations among several groups, including between spiders and carabids, but not between plants/spiders or plants/carabids. Finch & Löffler (2010) found strong correlations between plants and spiders, but not between carabids/spiders or plants/carabids. Our results add to the heterogeneity in findings, since we found even a negative correlation between plants and carabids. In our case this negative correlation seems to be driven by low plant species richness at the heavily grazed ridge that coincides with high diversity of carabid species. The ridge carabid fauna comprised many alpine specialists that are usually found at the margins of snow fields and snow pockets at higher altitudes (Holdhaus 1954; Franz 1970; Brandmayr *et al.* 2005; Paill & Kahlen 2009).

Moreover, comparing our results with those from other grassland ecosystems (Vessby *et al.* 2002; Sauberer *et al.* 2004; Finch & Löffler 2010), we found no consistent pattern for species richness correlation between the same taxa. Pairwise correlations were strong in some studies but absent or weak in others. These equivocal results call for caution in generalizing results from individual studies. One difficulty of finding predictive patterns of congruence between different taxa is the spatial scale at which relationships have been investigated (Pearson & Carroll 1999; Paavola *et al.* 2006; Hess *et al.* 2006; Gioria *et al.* 2011; Schuldt *et al.* 2015). Our study was conducted at a local scale, where correlations are often weaker than at larger scales (Paavola *et al.* 2006; Schuldt & Assmann 2010; Gioria, Bacaro & Feehan 2011). However, for many aspects of habitat management it is the local scale that is most important, and therefore the scale at which congruence analyses would be of high practical relevance.

4.5.3 Comparison of protected and unprotected plots

The designation of protected habitats of the Natura 2000 Special Area of Conservation is mainly based on vegetation characteristics. Not surprisingly, the selection seems appropriate for plants in protecting sites with high species richness and many habitat specialists. However, the effect does not generalize to carabids and spiders. Some of the plots with highest species richness and richness of important species in these taxa were outside protected habitats, especially on the ridge that held no specialized vegetation, but valuable communities of arthropods.

4.5.4 Implications for conservation

Our study shows that an identification of priority sites for conservation basing solely on vegetational aspects will not necessarily comprise the important sites for the arthropods. We show that there is no sufficient cross-taxon congruence between the three studied taxa at our study area. Moreover, we found significant negative effects between plant species richness and carabid species richness. Our results suggest that vascular plants are apparently no appropriate surrogates for spiders and carabids – two dominant and species rich taxa – in mountain grassland ecosystems. We support the notion of other authors who suggest that a range of taxonomic groups has to be used for prioritizing locations or actions for conservation (Grand *et al.* 2004; Wolters, Bengtsson & Zaitsev 2006; Zulka *et al.* 2014; Westgate *et al.* 2014; de Morais *et al.* 2018). In case of topographic diverse mountain ecosystem that often exhibit a diverse and specialised fauna with many endemic species, we think an approach covering different taxonomic groups is indispensable for conservation planning (Finch & Löffler 2010; Viterbi *et al.* 2013).

We are aware that time and money are limited for biodiversity assessments relevant to conservation. A practical solution would be to supplement large-scale vegetational mapping (following Annex 1 of the Natura 2000 Directive) with local sampling at selected plots of all different habitats with an expanded set of taxa. In the Alps, the efforts can be focused on taxa with a large number of endemic species, since these are often of greatest conservation concern. Here we see the groups of arthropods that we studied as one valuable complement to vascular plants, which is practicable especially as a reduced sampling design gives representative results (Harry *et al.* 2011). A taxonomically broader approach could give us better local knowledge about biodiversity and identification of specific sites that are of particular relevance for the conservation of often neglected taxa.

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5 Beitrag 3: Recovery of carabid beetle assemblages after cessation of intensive grazing in the German Alps: A six year study

Manuskript

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5.1 Abstract

Land use changes are an important issue in conservation in the European Alps, an area considered as biodiversity hotspot for Central Europe. We investigated the changes of Carabid beetle assemblages on a pasture during six years following the cessation of high-intensity grazing with sheep. We analysed changes in species richness as well as traits composition. Species richness increased with time, as well as abundance of carabid beetles, mean body length and number of traps where herbivore carabid species occurred. All these changes are indications of a recovery from intense grazing. However, proportion of beetles unable to fly and of mountain species sank over time, which was not expected and is discussed in detail. We also found different developments in some traits depending on the topographic situation of the sites and actual land use, which are discussed in detail and fit in the picture of changes due to altered land-use.

Carabid beetles performed well as indicators, showing significant results and thus have high importance for biodiversity conservation. Number of significant results is high in our study compared to other works, which is explained by the long term approach/character of our research project.

From a conservation perspective low intensity grazing is crucial for positive developments in large-scale mountain pastures. Abandonment resulted in positive effects over the time of our study. However, in areas below the treeline we suspect negative long-term effects of abandoning land use due to the increase of forest cover.

5.2 Introduction

The European Alps, as all mountain systems, are characterised by topographic and climatic heterogeneity, creating different habitats along the altitudinal gradient (Körner 2000). They are considered a biodiversity hotspot for Central Europe hosting a high amount of endemic species (Tribtsch 2004; Rabitsch 2009). Surrounded by intensively cultivated lowlands their conservation value is prominent (Gharadjedaghi et al. 2004).

The Alps have been influenced by anthropogenic land use over millennia (Bätzing 2005). Land use was traditionally practised with low intensity predominantly in large scale pastures of middle and high elevations. This led to an increase of grassland area at the expense of forests. These grasslands

are known to have a high conservation value due to their outstanding biodiversity (Bonavita et al. 1999; Stöcklin et al. 2007).

The Alps are currently going through profound changes, with subalpine pastures developing in diverging ways: whereas productive and accessible areas are nowadays managed more intensively, the declining profitability of labour-intensive agriculture in remote areas is causing widespread land abandonment, with consequent woodland expansion into previously grazed or otherwise managed areas (Cernusca 1999; Streifeneder and Ruffini 2007). Both developments are a cause for concern (Bonavita et al. 1999; Tasser and Tappeiner 2002).

Several studies investigated the effects of changes in mountain grassland ecosystems on biodiversity over time (cf. van Klink et al. 2015). However, to our knowledge only few studies deal with arthropods continuously sampled for more than three years after a change in land use.

Moreover, the effects of intensive land use are documented for some cases (Dennis et al. 2004; Dieker et al. 2011). But the effects of reduced land use intensity or abandonment on biodiversity of these mountainous grasslands are only poorly documented.

Additionally, analyses of species' traits, which promise a mechanistic understanding of the drivers of community and assemblage composition are of growing interest (Vandewalle et al. 2010; Aubin et al. 2013). However, only few investigations are known from mountain grassland ecosystems (Gobbi et al. 2015).

For decision making about preferable land use scenarios it is important to improve knowledge about consequences of different land use regimes and abandonment. This is especially true for protected areas in the context of Natura 2000 (Orlikowska et al. 2016). We already showed that conservation value differs strongly between grassland sites in these heterogeneous mountain habitats with respect of vascular plants and arthropods (Harry et al. submitted).

We chose carabid beetles as the study taxon as they are species-rich and harbour numerous species endemic to the Alps (Paill and Kahlen 2009). Carabids are known to be sensitive to land use changes (Lövei and Sunderland 1996; Kotze et al. 2011), taxonomy and ecology of the species are well known and thus they are often suggested as indicators (Luff 1996; Koivula 2011; Homburg et al. 2014).

Basing on data from a six year survey starting after a period of overgrazing we analysed (1) if and how the carabid assemblages change on different grassland sites, and (2) how species traits changed over time. (3) Finally, we gave suggestions for future habitat management.

5.3 Material and methods

5.3.1 Study area

The study was accomplished on the pasture “Alpe Einödsberg“ in the German Alps (47.32°N; 10.28°E). The study area involved altitudes between 1400 to 2000 meters above sea level and encompassed about 120 ha in total (Höfer et al. 2010). The whole study area is part of the “Allgäuer Hochalpen“, a territory listed as a Special Area of Conservation in the European conservation network Natura 2000 (Haslach 2011).

Most of the predominantly west-facing slopes consist of meadows dominated by *Nardus stricta*. Woodland belts are dominated by Norway spruce (*Picea abies*) and krummholz formed by *Alnus viridis* which are represented throughout the pasture zone. A ridge of 2 km length runs from north to south along the upper section of the pasture.

Life stock grazing can take place in the given altitudes only during summer months. In the first half of the 20th century the pasture was grazed with low intensity by cattle. Additionally the steep western slopes have been mowed from time to time. In the second half of the century this labour-intensive management was substituted by grazing with sheep. From the 1970ies onwards grazing intensity was high with more than 2000 sheep on the pasture (up to 15 sheep per hectare), and at times sheep were not adequately controlled by a shepherd. During that time grazing intensity differed strongly between single sites due to topographic reasons. Steeper parts of the pasture were subjects to a low grazing intensity. The impact of grazing was highest on the ridge, which was preferably used by resting livestock. Following a high concentration of faeces the vegetation on the ridge differs clearly from the surrounding grasslands.

In 2001 the management was changed, mainly because of intervention from nature conservation authorities: low intensity grazing by cattle was established on the predominant part of the pasture and a smaller part was abandoned.

5.3.2 Arthropod sampling

Arthropods were sampled with 6 pitfall traps per site. Traps consisted of plastic cups of 6 cm in diameter, filled with 5% acetic acid, 95% water and a drop of detergent to reduce surface-tension. Pitfall traps were installed at a distance of 6 m from each other. In order to protect the plastic cups from heavy rain and damage by the cattle, traps were constructed as metal tubes with transparent plastic cover (see Fig 1a in Höfer et al. 2010).

Pitfall traps were opened for two weeks during June (just after most snow had melted at the ridge), July and September. This exceeds the sampling protocol proved and suggested by Harry et al. (2011) to be adequate in mountain ecosystems. Between 2003 and 2008 a total of 34 sites were sampled. In the analyses presented in this contribution we integrated 19 sites which were intensively grazed until 2001 and sampled in at least four years: 15 sites were sampled every year, three sites in five years and one site in four years. Eight of the sampled sites are positioned on the ridge, eleven on slopes. While all sites were grazed in high intensity by sheep until 2000, ten of the sampled sites were grazed with low intensity by cattle from 2001 onwards, nine sites were abandoned.

Altogether we had 654 samples (catches in single traps pooled for each year). We excluded six samples from analyses due to damage by cattle trampling.

All carabids were identified to species level in the laboratory, with the exception of *Bembidion incognitum / deletum*, which cannot be identified with certainty. Both taxa were aggregated for the analysis.

5.3.3 Statistical Analyses

Our analyses focused on the changes of the carabid assemblages of the sites over time (year). We determined the overall change as well as differences according to the topographical position of the sites (from here on referred as ‘position’): sites on the ridge, which have been grazed more intensive by sheep in former times, in contrast to sites on the slopes. Additionally, we examined factual differences between the sites actually grazed with low intensity and sites which were abandoned (actual land use). Therefore, in all models we integrated ‘year’, ‘position’ and ‘actual land use’ as well as the interactions year : position and year : actual land use. As we had six traps per site we applied linear mixed effect models using the function lmer from the package lme4 (Bates et al. 2015), fitting site identity as a random effect. We used the package lmerTest (Kuznetsova et al. 2017) to approximate *p* values for fixed effects.

We fitted six linear mixed models for the response variables: species richness per trap, mean body length, proportion of mountain species and proportion of beetles from species that are incapable of flight. We extracted species characteristics (body size, altitudinal preferences, ability to fly) from the database carabids.org (Homburg et al. 2014) and additionally we used own unpublished data. Following Booij et al. (1994) we calculated the fresh body weight in mg for each species based on its mean body length in mm with the formula $\text{weight} = 0.05 * \text{body length}^{2.95}$ (in Booij et al. 1994

the formula is written incorrectly, but the correct formula can be deduced from their Fig.1). We summed up the body weights per site to the biomass of carabid beetles collected.

Response variables were transformed using square-root-transformation (species richness, mean body length, biomass) and angular (arcsine squareroot) transformation (proportion of mountain species). For proportion of beetles incapable of flight these transformations still were skewed, so we used the boxcox procedure as implemented in the package MASS to look for acceptable transformations and raised the power of 3.5, which gave a sufficient distribution for further analysis. As no satisfying data transformation was possible for trophic level (herbivore and carnivore) due to a high number of zero values, data were converted to binary data (i.e. whether or not herbivore species had occurred in a particular trap) and fitted logistic regressions to the data. Statistical Analyses were conducted using R 3.2.2 (R Development Core Team 2015).

5.4 Results

We collected 26,857 individuals and 51 species of carabid beetles.

In all models 'year' had a significant influence on the response variable. 'Position' had a significant influence on most response variables (except biomass and flight ability). In most cases the estimate for 'position' was highest (Tables 5.1 and 5.3), indicating strong difference in the response variable between ridge and slope (Figures 5.1 and 5.2). 'Year' had lower estimates, but yearly changes are given for the whole study period. The differences in changes over time are six times higher than the estimate. The more time has passed since 2001 (when high intensity grazing by sheep has been stopped), the more species and individuals we caught. Mean body length, biomass and occurrence of herbivory of carabid beetles increased during the study period. The proportion of mountain carabids and beetles without flight ability decreased over time (Table 5.2). However, working with abundance data of mountain carabids as well as flightless species we found an increase of abundances, but eurytopic carabids as well as species with flight ability increased stronger over time.

For some response variables we found significant effects of the interactions. On the ridge sites mean body length increased stronger over time than on the slopes. Moreover, on the latter sites herbivory occurred more often than on ridge sites. For the proportion of beetles without flight ability Figure 5.1 even points to opposing trends: We observed a decrease on the slopes, whereas on the ridge sites the given proportion increased over time.

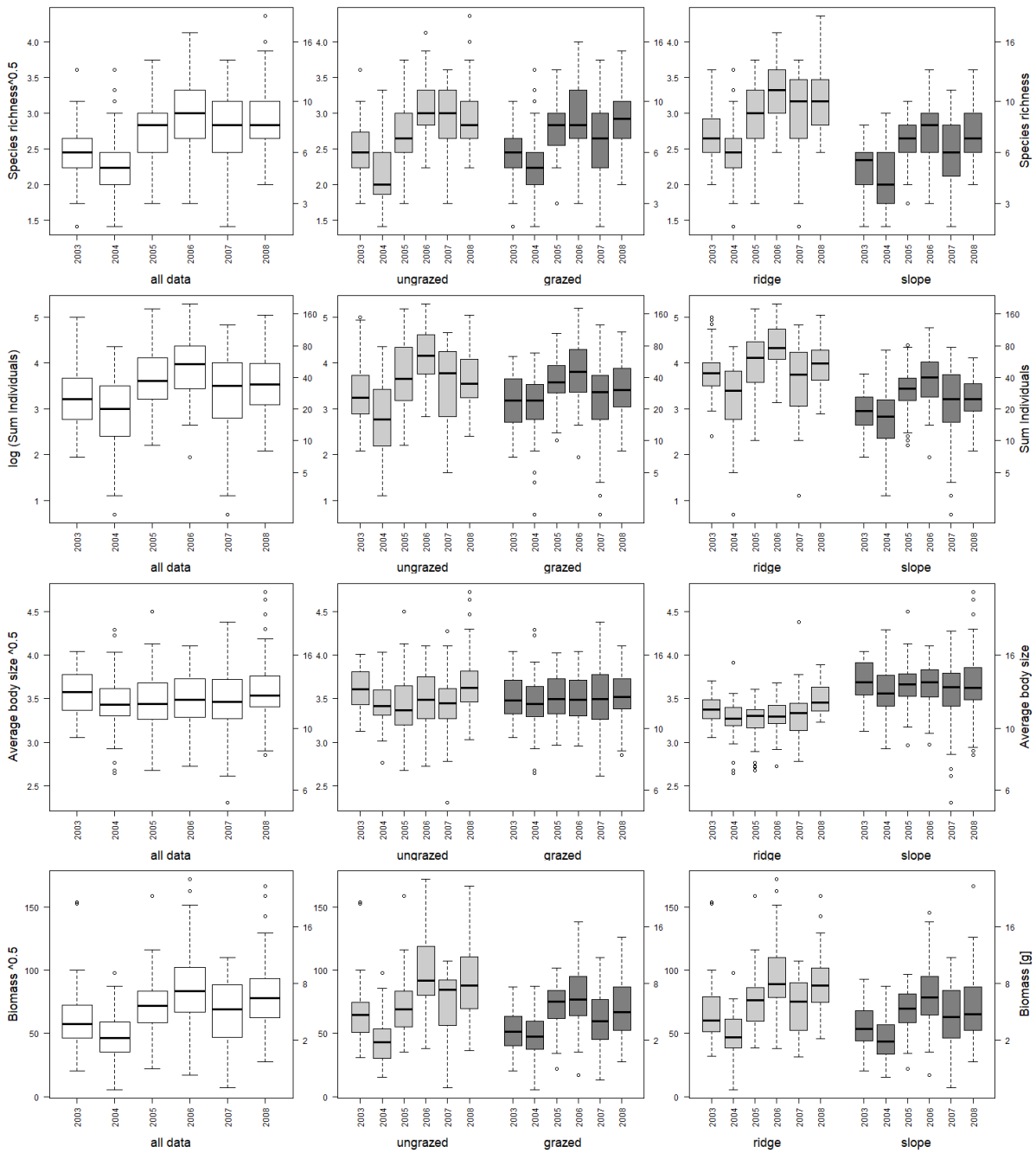


Figure 5.1 a-d: boxplots of response variables over time, given for all data and separated date of actually grazed and abandoned sites as well as ridge and slope sites. Data is given for transformed data (left y-axis), untransformed values can be derived from the second y-axis.

We also observed effects concerning ‘actual land use’: on the abandoned sites mean body length as well as biomass increased stronger than on grazed sites and herbivore carabid beetles were more widespread.

Table 5.1 (A-F): Results of the linear mixed effects models.

A. Species richness per trap (square-root-transformed)

Random effects variance: Between sites 0.04 Residual 0.16

	b	SE	df	t value	p
Intercept	2.7202	0.0509	13.1	53.46	< 0.001
position	-0.4533	0.1018	13	-4.46	< 0.001
year	0.1162	0.0098	634.7	11.81	< 0.001
actually grazed	0.0816	0.0840	30.5	0.97	0.339
position : year	-0.0222	0.0196	633.9	-1.13	0.258
actually grazed : year	-0.0186	0.0196	631	-0.95	0.342

B. Sum of individuals (log-transformed)

Random effects variance: Between sites 0.18 Residual 0.33

	b	SE	df	t value	p
Intercept	3.5	0.1	13.9	34.4	< 0.001
position	-0.68	0.2	13.9	3.34	0.005
year	0.08	0.01	634.1	5.74	< 0.001
actually grazed	0.2	0.15	57.6	1.34	0.185
position : year	0.01	0.03	633.3	0.5	0.618
actually grazed : year	-0.01	0.03	627.7	0.53	0.599

C. Mean body length (square-root-transformed)

Random effects variance: Between sites 0.02 Residual 0.05

	b	SE	df	t value	p
Intercept	3.48	0.04	16.4	96.18	< 0.001
position	0.32	0.07	16.4	4.38	< 0.001
year	0.02	0.01	635.7	2.83	0.005
actually grazed	0.02	0.05	54.7	0.32	0.748
position : year	-0.03	0.01	635	-3.04	0.002
actually grazed : year	-0.02	0.01	630.8	-2.08	0.038

Table 5.1 continued

D. Summed Biomass (square-root-transformed)

Random effects variance: Between sites 14.65 Residual 21.17

	b	SE	df	t value	p
Intercept	69.46	3.52	11.4	19.76	< 0.001
position	-10.82	7.03	11.4	-1.54	0.151
year	5.03	0.52	632.6	9.76	< 0.001
actually grazed	3.8	5.17	42.3	0.74	0.467
position : year	-1.32	1.03	631.6	-1.29	0.198
actually grazed : year	-2.62	1.02	625.2	-2.56	0.011

E. Proportion of individuals from mountain species (angular-transformed)

Random effects variance: Between sites 0.05 Residual 0.02

	b	SE	df	t value	p
Intercept	0.78	0.05	16.4	14.77	< 0.001
position	-0.43	0.11	16.4	-4.13	< 0.001
year	-0.03	0	631.2	-7.68	< 0.001
actually grazed	-0.01	0.05	277.1	-0.13	0.897
position : year	0	0.01	630.7	0.49	0.626
actually grazed : year	0.01	0.01	626.4	1.07	0.287

F. Proportion of individuals from species without flight ability (raised the power by 3.5)

Random effects variance: Between sites 0.03 Residual 0.04

	b	SE	df	t value	p
Intercept	0.6	0.04	16.2	13.64	< 0.001
position	0.02	0.09	16.2	0.26	0.799
year	-0.01	0	634.2	-2.29	0.022
actually grazed	-0.14	0.06	102.8	-2.5	0.014
position : year	-0.04	0.01	633.6	-3.67	< 0.001
actually grazed : year	0	0.01	628.2	0.17	0.869

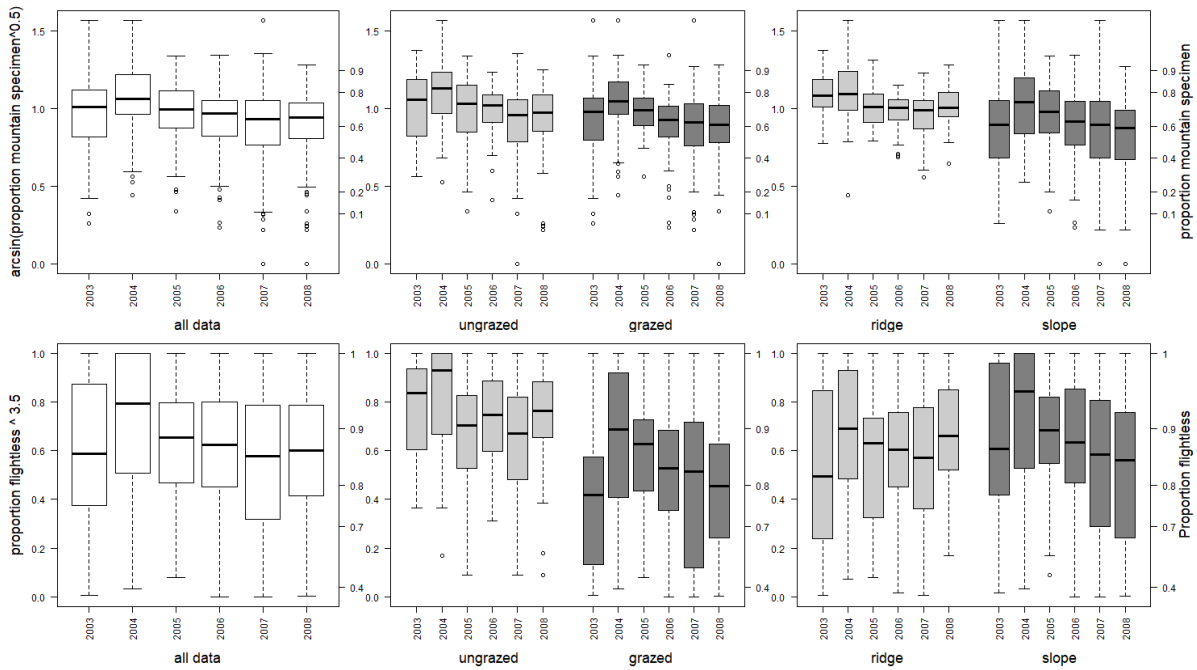


Figure 5.1 e-f: boxplots of response variables over time, given for all data and separated date of actually grazed and abandoned sites as well as ridge and slope sites. Data is given for transformed data (left y-axis), untransformed values can be derived from the second y-axis.

Table 5.2: Summary of significant results from all models.

response variable tested	position	year	actually grazed	position : year	actually grazed : year
Species richness per trap	higher on ridge	raises over time	-	-	-
Sum of individuals	higher on ridge	increases over time	-	-	-
Mean body length	larger on slope	increases over time	-	increases stronger on ridge	increases stronger on abandoned sites
Biomass	-	increases over time	-	-	increases stronger on abandoned sites
Proportion of individuals from mountain species	higher on ridge	decreases over time	-	-	-
Proportion of individuals from species without flight ability	-	decreases over time	higher on ungrazed sites	decreases stronger on slope	-
Traps with herbivore species	more on ridge	increases over time	-	increases stronger on slope	increases stronger on abandoned sites



Figure 5.2: Barplot of proportion of sites where presence of herbivore species was asserted (dark grey). Barplots are given for all data and separated data of actually grazed and abandoned sites as well as ridge and slope sites.

Table 5.3: Results of the logistic regression model.

Traps with herbivore species

	b	SE	z	p
Intercept	-0.09	0.21	-0.43	0.664
position	-1.68	0.42	-4.01	< 0.001
year	0.31	0.06	5.27	< 0.001
actually grazed	0.54	0.4	1.36	0.174
position : year	0.36	0.12	3.12	0.002
actually grazed : year	-0.34	0.12	-2.83	0.005

5.5 Discussion

In our six year study on mountain grasslands we were able to find effects for all response variables tested. Effects of ‘year’ were observed for all response variables, of ‘position’ (ridge vs. slope) for most response variables. Additionally, differing changes over time of the species traits were observed for ridge and slope sites as well as grazed and abandoned sites.

We found clear differences in the carabid assemblages between ridges and slopes: Species richness and abundance were both higher on ridge sites. For plants, we found a contrary development in our research area (Harry et al. submitted). Plant species richness was higher on slopes than on ridges. Different factors may influence species richness and abundances of carabid beetles on ridges and slopes.

The sites on the ridge have a higher primary production, especially due to faeces deposition by grazers. We observed significant higher aboveground plant biomass on these sites compared to the slopes (unpublished data).

Higher plant productivity may promote higher trophic levels and thus is often accompanied by higher abundances and species richness of both herbivore and predaceous species (Chen and Wise 1999).

This relationship is documented for different arthropods (Siemann 1998; van Klink et al. 2015) and also for carabid beetles (Söderström et al. 2001; Dennis et al. 2004, 2008). On the other hand, the higher plant productivity did not lead to a higher biomass of carabid beetles at the ridge sites.

A simple bottom up-effect of plant productivity on the biomass of carabid beetles seems unlikely. However, the ridges are at higher elevations than the slopes and the reduced biomass and abundance of carabids may be a consequence of lower temperature, as Binkenstein et al. (2018) documented for other predaceous taxa.

The sites on the ridge differ from the surrounding slopes and are characterized by longer snow cover (Harry et al. submitted). Those sites on the fringe of the snow fields and snow pockets inhabit a specialised alpine fauna of carabid beetles which have a strongly restricted distribution (Holdhaus 1954; Franz 1970; Schuldt and Assmann 2009; Homburg et al. 2014). Some of these species (e.g. *Oreonebria picea*) were found in our study.

The differences of the species traits mean body length and flight ability indicate stronger disturbance at the heavily grazed sites on the ridge. Mean body length is a diagnostic parameter for habitat disturbance and also land use intensity in carabid beetles (e.g. Ribera et al. 2001; Burel et al. 2004). Genera with large species, especially the genus *Carabus*, are indicators for less disturbed habitats (Tietze 1985; Cole et al. 2002). This is also true for grazed ecosystems: many authors reported smaller mean body length and lower abundances of *Carabus* species in intensely grazed pastures (Rushton et al. 1989; Blake et al. 1994; Dennis et al. 1997, 2002).

The focus of our study was the analysis of changes of carabid assemblages over time. After stopping highly intensive grazing, species richness increased as well as abundance. This is in line with most other studies dealing with the consequences of carabid beetles on different grazing intensities (Luff and Rushton 1989; Gardner et al. 1997; Dennis et al. 2004, 2008; Mysterud et al. 2010; Barton et al. 2011) and shows a recovery from heavy grazing pressure. Some studies found no effect of different grazing intensities on species richness or abundance (Söderström et al. 2001; Gobbi et al. 2015; Birkhofer et al. 2015) and single studies found an opposing effect on species richness and abundance (Grandchamp et al. 2005; García et al. 2009). These apparently

contradictory results may be explained in the sense of the intermediate Disturbance Hypothesis (Connell 1978): Species richness and abundance may increase up to a certain grazing intensity, but decrease towards highly intensive grazing pressures (or other agricultural treatments). A key issue is which grazing intensities are compared in the single studies. A recent review (van Klink et al. 2015) shows that in most cases arthropods are negatively affected by grazing intensity. Hence only grazing regimes with low intensity seem appropriate for protection of the most species rich arthropod groups. However, further empirical data of different grazing regimes is needed to get a more general picture, and many factors (e.g. time of grazing or fluctuating grazing intensities, Lenoir and Lennartsson 2010; Dieker et al. 2011) influence the outcome of management effects by grazing for arthropods.

Increased mean body length over time can be explained by land use intensity, as we discussed already for differences between ridge and slope sites. For this response variable we observed additional interactions. We found a stronger increase of body size at the ridge sites, which were formerly grazed in higher intensity. We also found a stronger increase on abandoned sites in comparison to sites actually grazed. Both these interactions support the idea that grazing intensity has a negative effect on body size.

As mean body length and abundance increases over time and especially on abandoned sites, the biomass increases analogously.

Proportion of flightless beetles decreased over time. This was unexpected, as a lower proportion of flightless beetles is often associated with disturbed areas, which is explained by the need for a higher dispersal power in habitats which are more disturbed (den Boer 1990; Cole et al. 2006; Gobbi et al. 2015; Hanson et al. 2016). However, abundance of flightless beetles increased over time, a decrease of proportion data is based on a stronger increase of beetles with flight ability. Additionally trends of ridge sites and slopes are opposing: on the slopes the proportion of flightless beetles decreased over time, whereas on the ridge sites proportion increased. As grazing was more intense on the ridge this might indicate that flight ability is a more important trait on sites with high land use intensity, while it is superimposed by other effects on sites where land use intensity is lower. Compared to other studies we found a high proportion of flightless beetles in all sites. In Central Europe most ground beetles species have flight ability and at least in open habitats most assemblages are dominated by species able to fly (Thiele 1977; Brandmayr 1991). However, in high altitudes a raised proportion of flightless beetles has been reported (Brandmayr 1991). Dispersal strategies on large scale grassland mountain habitats certainly differ to lowland areas with higher

land use intensity, where a higher importance of immigration to disturbed patches exists and many studies have been conducted (Hendrickx et al. 2007; Ewers 2008).

We found a high proportion of mountain species in the study area. Six of the species are listed as taxa with restricted range in the regional or national Red List (Lorenz 2003; Schmidt et al. 2016), some of them occurring in high densities (e.g. *Pterostichus jurinei* and *Pterostichus multipunctatus*). Few years ago, *Oreonebria picea*, a species of snow pockets, has been recorded in Germany for the first time (Huber et al. 2006). After stopping the intensive grazing, the proportion of mountain species declined over the years. Like for flight ability the decrease is only valid for proportion data, while abundances of mountain species increased. We expected that stenotopic mountain species would profit more than eurytopic species from a reduction of grazing intensity. One reason might be the effects of climate change. Brandmayr (2016) found a clear uphill-shift of mountain carabid species in the Alps within a few decades. Effects were particularly strong in open habitats, where some of the mountain species disappeared. Our data from six years give an indication for possible effects of climate change, but the study period is still too short for giving any evidence.

We observed an increase of herbivore carabid beetles over time, which is consistent with the hypothesis that primary consumer species should be more heavily affected by intense land use than carnivore species (Allombert et al. 2005; Mysterud et al. 2010; Hanson et al. 2016). Phytomass might be an important factor to understand patterns of herbivory occurrence, as the amount of phytomass increases with a reduction of grazing intensity. Sites on the ridge showed a higher phytomass and we found more herbivorous species there, despite of high grazing intensity. The possible relationship between phytomass and herbivorous carabid species is proved also by the finding that the abandoned sites have more of these carabid species/individuals than the extensively grazed sites.

From a conservation perspective we appreciate the stopping of intensive and uncontrolled sheep grazing in mountain grassland. We interpret the changes of the carabid assemblages as a recreation from heavy land use, with increasing species richness, abundances, mean body length and biomass. Although we observed decreasing proportion of flightless and mountain beetles, abundances of both groups increased. Future changes of assemblage structure regarding these two traits has to be observed to get a more precise evaluation.

We found some differences between abandoned and grazed sites within the few years of our study: on the abandoned sites, the same processes happen, but development is faster. Short-term evaluation of the abandoned sites is positive. However, we have to be conscious that further long-term changes will occur in the area, and especially on the abandoned sites succession towards forests will take place. Tyler (2008) found high conservation values of young fallows (especially less than 10 years old) for carabids in northern Europe, but old fallows were species-poor. Studies from the European Alps show a higher conservation value of grassland habitats in comparison to forests on the same altitude for diverse animals (Stöcklin et al. 2007) and also for carabids (Bonavita et al. 1999). We assume that low intensity grazing, associated with measures to keep the area open, will imply a better long-term development compared to abandonment (cf. Nascimbene et al. 2014). For future management of mountain pastures we promote maintenance of (respectively reduction to) low intensity grazing.

The reaction of ground beetles to abandonment or reduced grazing intensity are mostly unknown. With our design of sampling sites over six years we were able to identify significant trends over time. Fluctuations of population densities of carabid species exceed up to three powers of ten (den Boer and van Dijk 1994). Therefore in short-term studies it is very difficult to distinguish between annual fluctuations and trends over time. As a consequence, we strongly recommend long-term studies to evaluate success of conservation measures, especially for effects which develop slowly over time

Carabid beetles performed well as indicators for land use change. Spiders did not show significant reactions in our study (Höfer and Harry 2009). Carabid beetles are known to react fast and strong on land use changes (Koivula 2011; Barton et al. 2011). In addition, carabids are one of the richest and most abundant components of ground dwelling arthropods and comprise a large number of endemic species in the Alps (Paill and Kahlen 2009). Thus especially in mountain ecosystems they are an important group for biodiversity conservation.

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5.7 References

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7 Curriculum vitae

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8 Publikationen

- Anthes N., Harry I. et al. (2002): Notes on migration dynamics and biometry of the Wood Sandpiper (*Tringa glareola*) at the sewage farm of Münster (NW Germany). *Ring* 24(1): 41–56.
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landwirtschaftliche Nutzung. Angewandte Landschaftsökologie. Landwirtschaftsverlag. Bonn
- Bad Godesberg: 304–307.

9 Erklärung

Hiermit erkläre ich, dass ich bisher anderweitig keine Dissertation eingereicht, einen Dissertationsentwurf vorgelegt oder einen Antrag auf Zulassung zur Promotion gestellt habe.

Hiermit erkläre ich, dass die Dissertation in der gegenwärtigen oder einer anderen Fassung noch keinem anderen Fachbereich zur Begutachtung vorgelegen hat.

Ich versichere, dass ich die eingereichte Dissertation „Ökologische Untersuchung und Bewertung der Extensivierung einer Hochweide: Eine Fallstudie an Laufkäfern der Alpe Einödsberg im Allgäu“ selbständig und ohne unerlaubte Hilfsmittel verfasst habe. Anderer als der von mir angegebenen Hilfsmittel und Schriften habe ich mich nicht bedient. Alle wörtlich oder sinngemäß den Schriften anderer Autorinnen oder Autoren entnommenen Stellen habe ich kenntlich gemacht.

Ingmar Harry