Endbericht

Biodiversität und nachhaltiges Management von Steinbrüchen in Zeiten des globalen Wandels

UNIVERSITÄT
OSNABRÜCK

2022

Titelseite

Heterogener, artenreicher Steinbruch mit Kleingewässer. Typische Arten derartiger Steinbrüche sind (im Uhrzeigersinn) Argus-Bläuling (*Plebejus argus*), Kreuzkröte (*Epidalea calamita*), Zierliches Tausendgüldenkraut (*Centaurium pulchellum*), Heide-Blattschneiderbiene (*Megachile ericetorum*) und Flussregenpfeifer (*Charadrius dubius*).

Fotos: Hauptbild und Kreuzkröte – Marcel Kettermann, übrige Bilder – Thomas Fartmann.

Endbericht (DBU-AZ 34381/01)

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1 Einleitung

1.1 Rückgang der Biodiversität in Zeiten des globalen Wandels

Seit der Industrialisierung und insbesondere nach dem 2. Weltkrieg hat der Mensch die Umwelt mit zuvor nicht gekannter Geschwindigkeit verändert (Rockström et al. 2009). Dies hatte dramatische Auswirkungen auf die Biodiversität. Gegenwärtig sind die Aussterberaten von Pflanzen- und Tierarten tausendmal höher als es natürlicherweise der Fall wäre (De Vos et al. 2014, Pimm et al. 2014). Entsprechend prognostizieren Forscher ein sechstes Massenartensterben, sollte diese Entwicklung wie bisher voranschreiten (Barnosky et al. 2011).

Als Hauptverursacher des globalen Artensterbens wird der Mensch angesehen. Insbesondere Änderungen der Landnutzung haben erheblich zum Verlust der Artenvielfalt beigetragen (Sala et al. 2000). Seit Ende des letzten Jahrtausends steht zudem zunehmend die Bedeutung des anthropogenen Klimawandels für den Rückgang der Artenvielfalt im wissenschaftlichen Fokus (Essl & Rabitsch 2013, Streitberger et al. 2016). Als Hauptverursacher des globalen Artensterbens wird der Mensch angesehen. Insbesondere Änderungen der Landnutzung haben erheblich zum Verlust der Artenvielfalt beigetragen (Foley et al. 2005, IPBES 2019, Cardoso et al. 2020).

Der Landnutzungswandel hat zu gravierenden quantitativen und qualitativen Veränderungen der mitteleuropäischen Landschaften geführt (Gatter 2000, Fartmann 2006, 2017, Ellenberg & Leuschner 2010, Poschlod 2017, Fartmann et al. 2021). Welt- und europaweit den größten Flächenzuwachs verzeichnen Siedlungen (United Nations 2010). Aktuelle Szenarien gehen von einer Zunahme der Stadtbevölkerung von gegenwärtig 3,5 Mrd. auf 6,3 Mrd. Menschen im Jahr 2050 aus. Verbunden mit der massiven Zunahme der Siedlungs- und Verkehrsfläche in Mitteleuropa ist eine dramatische Abnahme von extensiv oder kaum genutzten, nährstoffarmen Habitaten (Fartmann 2006, 2017, Fartmann et al. 2021). Infolgedessen kommen derartige Lebensräume und ihre Biozönosen heute häufig nur noch kleinflächig und isoliert vor; entsprechend werden solche Landschaften als fragmentierte Landschaften bezeichnet. Der Fortbestand der Lebensgemeinschaften in den Habitatfragmenten ist zudem oft durch eine verringerte Habitatqualität aufgrund von Nutzungsintensivierung oder -aufgabe (Fartmann 2017, Fartmann et al. 2021), Randeffekten aufgrund geringer Flächengröße (Fahrig 2003, Fartmann et al. 2021) und atmosphärischen Stickstoffeinträgen (WallisDeVries & Bobbink 2017, Kurze et al. 2018) gefährdet. Obwohl sich die Flächenausdehnung von landwirtschaftlich genutzten Flächen in Deutschland seit dem 2. Weltkrieg nur geringfügig geändert hat (Fartmann 2006, 2017), weisen Habitate der Agrarlandschaften heute die größten Rückgänge der Biodiversität auf (Donald et al. 2006, Henle et al. 2008, Kleijn et al. 2009, Leuschner et al. 2013).

Die Erhaltung und Förderung der Artenvielfalt ist weltweit spätestens seit der Verabschiedung des Übereinkommens über die biologische Vielfalt (*Convention on Biological Diversity*) in Rio de Janeiro 1992 das zentrale Thema des Naturschutzes (Heywood 1995). Entsprechend hat eine Vielzahl von Ländern nationale Strategien zum Schutz der biologischen Vielfalt verabschiedet, so auch Deutschland (BMU 2007). Das Ziel, den Artenrückgang bis 2010 zu stoppen, ist allerdings deutlich verfehlt worden (Butchart et al. 2010, Piechocki et al. 2010).

In Deutschland fehlen generell zukunftsfähige Konzepte zur Erhaltung der Artenvielfalt, die sowohl die Auswirkungen des Landnutzungs- als auch des Klimawandels hinreichend berücksichtigen (Fartmann et al. 2012, Streitberger et al. 2016). Dies gilt auch für Steinbrüche, die aufgrund des globalen Baubooms und damit zusammenhängend einer stark gestiegenen Nachfrage nach Baumaterial – wie Zement oder Steinen (United Nations 2010, 2014, Harder 2010) – eine zunehmend größere Bedeutung erlangen.

1.2 Biodiversität von Steinbrüchen

Lange Zeit wurden Steinbrüche mit Landschaftszerstörung und Verlusten der Artenvielfalt gleichgesetzt (Gilcher 1995, Poschlod et al. 1997, Gilcher & Tränkle 2005, Tropek et al. 2010). Entsprechend ist es immer noch gängige Praxis Steinbrüche nach Abschluss der Abbautätigkeit zu verfüllen und aufzuforsten (Krauss et al. 2009, Tropek et al. 2010, Stichling [Lhoist Germany – Rheinkalk GmbH] mdl. Mitt., eig. Beob.). Erst seit Ende der 1990er-Jahre sind Steinbrüche und ihre Bedeutung für den Biodiversitätsschutz stärker in den wissenschaftlichen Fokus gerückt (z.B. Wheater & Cullen 1997, Beneš et al. 2003). Aktuelle Studien an Spinnen (Tropek & Konvička 2008, Tropek et al. 2008), Libellen (Distel 2012, Kettermann 2017), Heuschrecken (Kettermann & Fartmann 2018) und Tagfaltern (Beneš et al. 2003) belegen die große Bedeutung von Steinbrüchen für wärmeliebende und gefährdete Arten.

Obwohl jüngst wiederholt die große Bedeutung von genutzten und aufgegebenen Steinbrüchen für den Naturschutz gezeigt wurde, gibt es weiterhin massive Kenntnisdefizite zur Biodiversität von Steinbrüchen und zum nachhaltigen Management. Detaillierte und gut replizierte Studien zur Biodiversität von Steinbrüchen und den entscheidenden Umweltparametern liegen aus Mitteleuropa nahezu nur für Tschechien vor (Beneš et al. 2003, Novak & Konvička 2006, Tropek & Konvička 2008, Tropek et al. 2008, 2010). Aus Deutschland existieren entsprechende Arbeiten lediglich durch die eigenen Vorarbeiten (Libellen: Distel 2012, Kettermann 2017; Heuschrecken: Kettermann & Fartmann 2018) und eine Studie zu Wildbienen von Krauss et al. (2009). Bei letzterer erfolgte allerdings im Gegensatz zu den eigenen Arbeiten zu Libellen (Steinbruchgewässer vs. Gewässer in der Normallandschaft) kein Vergleich mit anderen Habitaten der umgebenden Landschaft.

In den wichtigen Übersichtsarbeiten (Gilcher 1995, Poschlod et al. 1997, Gilcher & Tränkle 2005) wird Steinbrüchen auch eine hohe Bedeutung für den Erhalt der Artenvielfalt bei Pflanzen, Amphibien und Vögel zugesprochen. Entsprechende empirische Studien zur Biodiversität dieser Gruppen in Steinbrüchen und Vergleichshabitaten fehlen ebenso wie bei den Wildbienen. Auch unsere darauf aufbauenden Kenntnisse zum Management und zur Renaturierung von Steinbrüchen sind immer noch gering. Im Gegensatz zu vielen anderen Lebensraumtypen werden Steinbrüche beispielsweise im Renaturierungs-Grundlagenwerk von Zerbe & Wiegleb (2009) überhaupt nicht behandelt.

1.3 Persistenz von Arten in fragmentierten Landschaften

Die Faktoren, die das Vorkommen von Arten in unseren fragmentierten Landschaften bestimmen hängen stark von der Mobilität bzw. Populationsstruktur der Taxa ab (Fartmann 2017). Arten mit geringer Mobilität (z.B. Pflanzen oder flugunfähige Insekten) bilden häufig geschlossene Populationen. Sie sind in der Lage selbst in isolierten Habitaten über längere Zeiträume zu überleben, sofern diese groß genug sind und eine günstige Habitatqualität aufweisen. Für eine Ausbreitung und Neubesiedlung von Habitaten sind aber auch diese Arten auf eine gute Vernetzung der Habitate angewiesen. Flugfähige und deutlich mobilere Arten weisen dagegen eher Metapopulationsstrukturen auf. Ihr Vorkommen hängt von der Habitatqualität, Flächengröße *und* Isolation der Habitate ab (Thomas et al. 2001, Anthes et al. 2003, WallisDeVries 2004, Eichel & Fartmann 2008, Stuhldreher & Fartmann 2014).

Basierend auf den zuvor gemachten Ausführungen können Arten, die geschlossene Populationen aufweisen als Indikatoren für die Habitatqualität herangezogen werden (Fartmann 2017). Metapopulationsarten gelten darüber hinaus als Indikatoren für die Landschaftsstruktur: Sie sind auf ein Netz von Habitaten mit günstiger Qualität und ausreichender Größe in räumlicher Nachbarschaft angewiesen. Die Übergänge zwischen Arten mit geschlossenen Populationen und Metapopulationen sind teilweise fließend. Gleiches gilt folglich für ihre indikatorische Bedeutung.

Unsere Kenntnisse zur Bedeutung der drei Schlüsselfaktoren Habitatqualität, Flächengröße, Isolation/Landschaftsstruktur für das langfristige Überleben der Biozönosen von Steinbrüchen sind bislang unzureichend. Wiederholt nachgewiesen wurde die hohe Bedeutung von frühen Sukzessionsstadien in Steinbrüchen für wärmeliebende und gefährdete Arten (Beneš et al. 2003, Tropek & Konvička 2008, Tropek et al. 2008, Kettermann & Fartmann 2018). Zudem hat die Flächengröße ein positiven Einfluss auf die Diversität der Wildbienenzönose (Krauss et al. 2009) und das Vorkommen der Blauflügeligen Sandschrecke (*Sphingonotus caerulans*) (Kettermann & Fartmann 2018). Ein Einfluss der umgebenden Landschaft auf die Diversität der Zönosen in den Steinbrüchen konnte für Pflanzen (Novak & Konvička 2006) und Tagfalter (Beneš et al. 2003) nachgewiesen werden.

Vertiefende Untersuchungen zu den Faktoren, die die Habitatqualität in Steinbrüchen für die Indikatorgruppen dieses Projektes (Pflanzen, Amphibien, Tagfalter und Wildbienen) bestimmen fehlen bislang allerdings. Gleiches gilt für die Kenntnisse zum Einfluss der Flächengröße und der umgebenden Landschaft auf die Zönosen dieser Organismengruppen in Steinbrüchen. Entsprechend schwer fällt es bislang, langfristig wirksame und nachhaltige Maßnahmenkonzepte für die Erhaltung der Biodiversität von Steinbrüchen in unseren fragmentierten Landschaften zu entwickeln.

1.4 Ziele des Projektes

Basierend auf den zuvor gemachten Ausführungen soll am Beispiel von Pflanzen, Amphibien, Tagfaltern und Wildbienen gezeigt untersucht werden, welche Faktoren der Habitat- und Landschaftsqualität für die Ausbildung artenreicher Biozönosen in Steinbrüchen verantwortlich sind. Ein besonderer Fokus liegt hierbei auf der Betrachtung gefährdeter Arten. Aufbauend auf den eigenen Studien und Erkenntnissen aus Abschlussarbeiten zu Vögeln und Libellen werden wissenschaftlich-fundierte Handlungsempfehlungen zum biodiversitätsfördernden und nachhaltigen Management von Steinbrüchen in Mitteleuropa erarbeitet.

2 Untersuchungsgebiet

Als Untersuchungsgebiet (UG) dient eines der wichtigsten Gesteinsabbaugebiete Europas – Westfalen und die östlich angrenzenden Regionen Niedersachsens und Hessens (Abb. 1) (IG Teuto 2000, Grothues 2007). Das UG umfasst die naturräumlichen Haupteinheiten Westfälische Tieflandsbucht, Süderbergland sowie das Weser- und Weser-Leine-Bergland (BfN 2012). Von West nach Ost beinhaltet es die sieben Zentren des Gesteinsabbaus im UG, nämlich die Teiluntersuchungsgebiete (TUG) Tieberg/Waldhügel bei Rheine, Teutoburger Wald, Beckumer Berge, östliche Hellwegbörden, Diemeltal, Lipperland und Weser-Leine-Bergland. Insgesamt existieren in den TUG 117 Steinbrüche mit einer Mindestgröße von 5 ha.

Die Meereshöhe nimmt von 60 mNN im Nordwesten nach Nord- und Südosten auf bis zu 460 mNN zu. In den vier TUG der Westfälischen Tieflandsbucht werden Kreidekalke abgebaut (IG Teuto 2000, Grothues 2007). Die Steinbrüche des Oberen Diemeltals dienen der Gewinnung von devonischen Massenkalken, Zechsteinkalken und Diabas (Fartmann 2004). Im Unteren und Mittleren Diemeltal sowie Lipperland handelt es sich um Muschelkalk- bzw. Basalt- und im Weser-Leine-Bergland um Sandsteinbrüche (Fartmann 2004, Rothe 2006).

Das Klima im UG ist subatlantisch (MURL NRW 1989). Die Jahresniederschläge variieren in Abhängigkeit von der Meereshöhe und Regenstau-/schatteneffekten an den Gebirgszügen zwischen 600 und 1.000 mm pro Jahr (langjähriges Mittel: 1981–2010; DWD, schriftl. Mitt.). Besonders niedrig sind die Werte daher im Mittleren Diemeltal; sehr hohe Niederschlagsmengen werden im Oberen Diemeltal und Weser-Leine-Bergland erreicht. Die mittlere Jahrestemperatur bewegt sich zwischen 6 und 9,5 °C (langjähriges Mittel: 1981–2010; DWD, schriftl. Mitt.). Besonders milde Bedingungen herrschen in den tieferen Lagen der Westfälischen Tieflandsbucht; durch ein auffallend kühles Klima ist das Obere Diemeltal gekennzeichnet (Fartmann 2004).

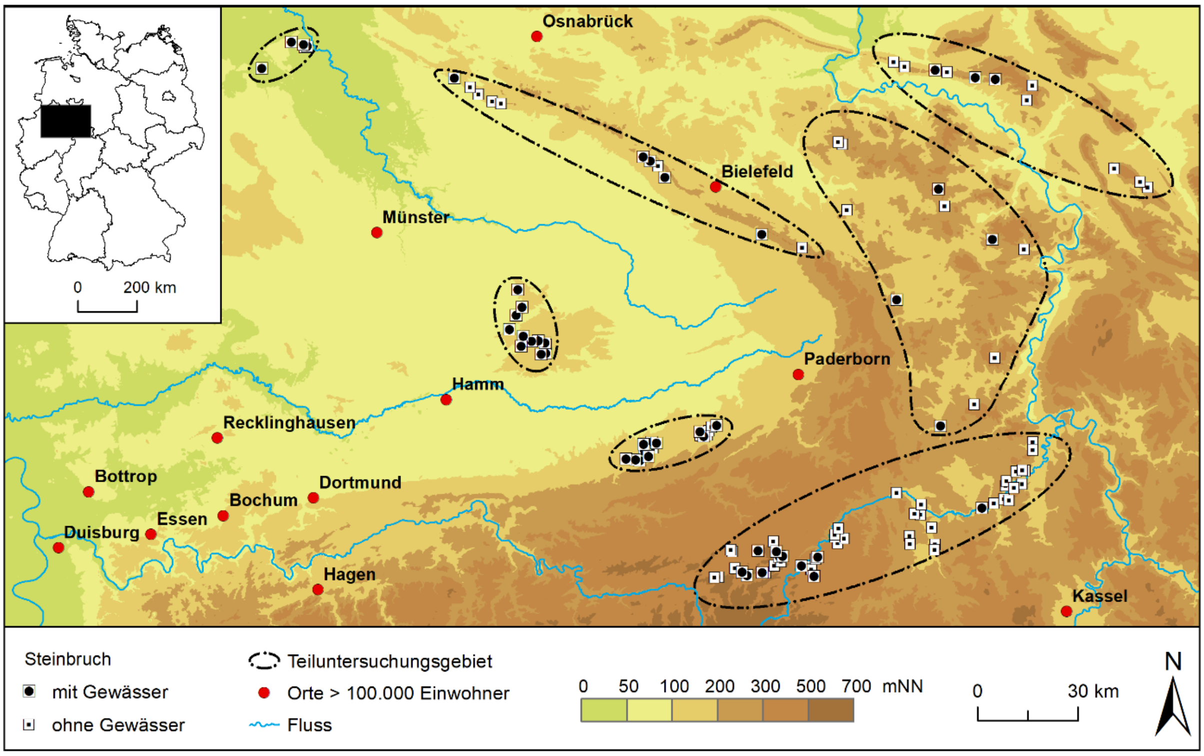

Abb. 1: Lage der Untersuchungsgebiete in Westfalen und angrenzenden Gebieten.

Das UG ist überwiegend durch intensive landwirtschaftliche Nutzung gekennzeichnet. Eine Sonderrolle nimmt das Diemeltal ein, da hier mit einer Ausdehnung von 750 ha noch großflächig Kalkmagerrasen vorkommen (Fartmann 2004).

3 Pflanzen – Vergleich der Zönosen von Kleingewässern in Kalksteinbrüchen und in der Normallandschaft

3.1 Material und Methoden

Untersuchungsgebiet: Westfälische Bucht und Ostwestfalen.

Versuchsdesign: Vergleich von 15 Kleingewässern in Steinbrüchen mit 15 Kleingewässern in der Normallandschaft; zwei Erfassungstermine Ende Mai und Anfang Juli.

3.2 Ergebnisse

Umweltbedingungen

Die Habitatqualität von Kleingewässern in Steinbrüchen unterschied sich deutlich von der der Kontrollgewässer (Tab. 1). Steinbruchgewässer wiesen eine viel geringere Baumschichtdeckung am Ufer und damit eine deutlich höhere Sonnenscheindauer auf als die Kontrollgewässer. Die amphibische Zone nahm fast zwei Drittel der Fläche der Steinbruchgewässer ein und machte somit einen mehr als doppelt so hohen Anteil des Gewässers aus wie bei den Kontrollen. Entsprechend waren auch die Wasserstandsschwankungen an den Steinbruchgewässern um ein Vielfaches höher. Darüber hinaus waren die Steinbruchgewässer durch höhere Offenbodenanteile am Ufer, eine höhere Deckung der emersen Vegetation (Röhrichtpflanzen und Juncaceae) und Unterwasservegetation (Armleuchteralgen), aber eine geringere Deckung der Schwimmblattvegetation und der Kräuter innerhalb der emersen Vegetation gekennzeichnet als die Kontrollgewässer.

Die Landschaftsqualität unterschied sich dagegen kaum zwischen den beiden Gewässertypen (Tab. 1). Die Steinbruchgewässer waren lediglich etwas höher gelegen.

Phytozönosen in Abhängigkeit von den Umweltbedingungen

Insgesamt konnten 156 verschiedene Pflanzenarten (118 Gefäßpflanzen, 33 Moose und 5 Armleuchteralgen) in den Gewässern nachgewiesen werden. Davon waren 28 Arten auf der Roten Liste Nordrhein-Westfalens aufgeführt.

Alle betrachteten Pflanzengruppen (alle Arten, Gefäßpflanzen, Moose, Armleuchteralgen) wiesen sowohl bei allen Arten als auch bei gefährdeten Arten höhere Artenzahlen in Steinbruchgewässern als in Kontrollgewässern auf (Abb. 2). Lediglich bei der generell artenarmen Gruppe der Armleuchteralgen unterschied sich die Anzahl gefährdeter Arten zwischen den beiden Gewässertypen nicht.

Die Steinbruchgewässer wiesen insgesamt 22 Indikatorarten, die Kontrollgewässer lediglich neun auf (Tab. 2). Unter den Indikatorarten der Steinbruchgewässer gelten zwei, *Centaurium pulchellum* und *Fissidens adianthoides*, als in Nordrhein-Westfalen gefährdet.

Tab. 1: Übersicht über die Umweltparameter (arithm. Mittel [Ø] ± Standardfehler [SF], Minimum und Maximum) in Steinbruchgewässern (Steinbruch, *N* = 15) und Kontrollgewässern (Kontrolle, *N* = 15). Unterschiede zwischen den beiden Gewässertypen wurden mittels generalisierter linearer gemischter Modelle (GLMM; Fehlerstruktur: negativ-binomial für Zähldaten, proportional-binomial für Deckungen) mit 'Teiluntersuchungsgebiet' als Zufallsfaktor analysiert. Statistische Unterschiede sind folgendermaßen angegeben: n.s. = nicht signifikant; $P \geq 0,05$; * $P < 0,05$; ** $P < 0,01$; *** $P < 0,001$.

Parameter	**Steinbruch**		**Kontrolle**		***P***
	Ø ± SF	Min.–Max.	Ø ± SF	Min.–Max.	
Habitatqualität					
Gewässergröße [m^2][1]	3.033 ± 868	32–14,630	1.064 ± 350	78–5,527	n.s.
pH[2]	7,1 ± 0,1	7–8	6,9 ± 0,2	7–8	n.s.
Leitfähigkeit [µS/cm][2]	456,1 ± 39,0	204–733	563 ± 60,9	218–974	n.s.
Sonnenschein Juli [h/Tag][3]	13,9 ± 0,5	10–16	5,7 ± 1,0	1–16	***
Wasserstandsschwankungen [cm][4]	29,9 ± 13,2	0–180	6,5 ± 1,8	0–25	**
Diversitätsindex[5]					
Gewässer	9,5 ± 0,5	5–12	7,5 ± 0,6	4–11	n.s.
Ufer	3,2 ± 0,2	2–4	3,1 ± 0,2	2–4	n.s.
Deckung Ufer [%]					
Bäume	4,0 ± 1,3	0–15	30,0 ± 4,3	0–50	***
Sträucher	19,0 ± 4,1	5–65	21,2 ± 4,7	0–60	n.s.
Feldschicht	42,8 ± 6,2	2,5–70,0	45,3 ± 5,7	5–95	n.s.
Offenboden	35,0 ± 7,9	5–95	4,8 ± 2,0	0–30	***
Deckung Gewässer [%]					
Amphibische Zone	65,0 ± 5,8	35–100	32,3 ± 6,9	5–100	**
Offene Wasserfläche	45,3 ± 7,8	5–95	43,7 ± 9,1	0–95	n.s.
Schwimmblattvegetation	6,8 ± 3,3	0–50	40,2 ± 8,7	2,5–90,0	**
Emerse Vegetation	48,7 ± 7,4	5–95	16,8 ± 3,7	2,5–60,0	***
Röhrichtpflanzen	20,8 ± 5,3	0–70	4,2 ± 2,7	0–40	***
Juncaceae	13,3 ± 2,0	2,5–25,0	1,8 ± 0,7	0–10	***
Cyperaceae	9,8 ± 3,7	0–55	2,8 ± 0,9	0–10	n.s.
Kräuter	1,5 ± 0,5	0–5	5,2 ± 1,2	0–15	***
Moose	4,8 ± 1,5	2,5–25,0	3,5 ± 0,3	2,5–5,0	n.s.
Unterwasservegetation	44,7 ± 5,3	15–85	21,3 ± 6,4	5–90	**
Kräuter	18,3 ± 3,5	2,5–55,0	16,2 ± 5,9	2,5–80,0	n.s.
Armleuchteralgen	21,0 ± 3,7	2,5–45,0	0 ± 0,0	0–0	***
Grünalgen	6,3 ± 0,9	2,5–15,0	5,7 ± 0,9	2,5–10,0	n.s.
Landschaftsqualität					
Meereshöhe [m NN][6]	181,0 ± 14,3	98–289	158 ± 16,7	91–287	*
Jahresmitteltemperatur [°C][7]	9,2 ± 0,1	8,1–9,8	9,3 ± 0,1	8,5–9,9	n.s.
Mittlerer Jahresniederschlag [mm][7]	907 ± 20	815–1.088	947 ± 75	800–1.945	n.s.
Gewässerkonnektivität [m][8]	783 ± 223	47–2.479	697 ± 137	27–1.595	n.s.

[1] Berechnet anhand von Luftbildern in ArcGIS 10.3.1.

[2] Ermittelt mit einer Messsonde (Hanna HI 98129).

[3] Ermittelt mit einem Horizontoskop; arithmetisches Mittel der Messwerte im N, E, S und W des Gewässers (Holtmann et al. 2017).

[4] Ermittelt mittels eines Pegels.

[5] Shannon-Index der Strukturtypen.

[6] Die Meereshöhe wurde anhand topgraphischer Karten bestimmt.

[7] Langjähriges Mittel (1981–2010) basierend auf Rasterdaten (1 km^2) des Deutschen Wetterdiensts.

[8] Geometrisches Mittel der Entfernung zu dne nächsten drei Stillgewässern

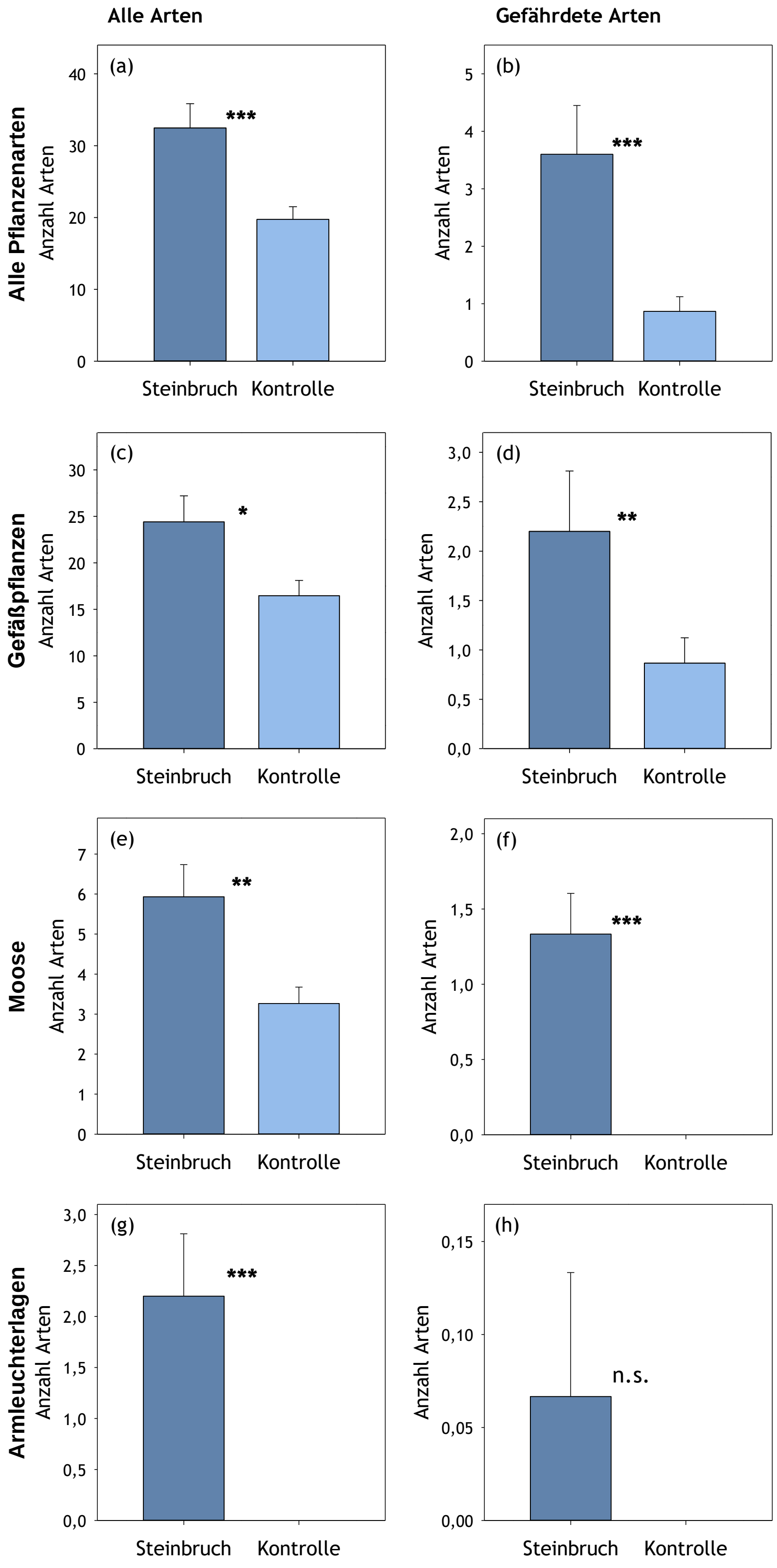

Abb. 2: Arithmethisches Mittel ± Standardfehler (SF) der Anzahl aller Arten (a), gefährdeter Arten (b), aller Gefäßpflanzenarten (c), gefährdeter Gefäßpflanzenarten (d), aller Moosarten (e), gefährdeter Moosarten (f), aller Armleuchteralgen (g) und gefährdeter Armleuchteralgen (h) in Steinbruchgewässern (Steinbruch, *N* = 15) und Kontrollgewässern (Kontrolle, *N* = 15). Unterschiede zwischen den beiden Gewässertypen wurden mittels generalisierter linearer gemischter Modelle (GLMM; Fehlerstruktur: negativ-binomial für Zähldaten, proportional-binomial für Deckungen) mit 'Teiluntersuchungsgebiet' als Zufallsfaktor analysiert. Statistische Unterschiede sind folgendermaßen angegeben: n.s. = nicht signifikant; $P \geq 0,05$; * $P < 0,05$; ** $P < 0,01$; *** $P < 0,001$.

Tab. 2: Ergebnisse der Indikatorartenanalyse: Pflanzenindikatorarten der Steinbruch- (Steinbruch, N = 15) und Kontrollgewässer (Kontrolle, N = 15). Es sind nur Arten mit einem signifikanten Indikatorwert (IW) dargestellt. Gefährdete Arten sind in Fettdruck hervorgehoben. % = Stetigkeit. Statistische Signifikanz ist folgendermaßen angegeben: $P \geq 0{,}05$; * $P < 0{,}05$; ** $P < 0{,}01$; *** $P < 0{,}001$.

Indicatorarten	***P***	**Gewässertyp**			
		Steinbruch		Kontrolle	
		IW	%	IW	%
Gefäßpflanzen				.	
Betula pendula	***	82	66,7	.	0,0
Calamagrostis epigejos	**	74	60,0	.	6,7
Centaurium pulchellum	*	58	33,3	.	0,0
Eleocharis vulgaris	*	72	66,7	.	20,0
Epilobium tetragonum subsp. *tetragonum*	*	64	53,3	.	6,7
Eupatorium cannabinum	*	64	46,7	.	6,7
Juncus articulatus	***	93	93,3	.	0,0
Plantago major subsp. *intermedia*	*	70	66,7	.	13,3
Prunella vulgaris	**	73	60,0	.	0,0
Salix caprea	***	90	93,3	.	6,7
Salix cinerea	*	72	73,3	.	20,0
Schoenoplectus lacustris	*	64	53,3	.	6,7
Typha latifolia	*	72	66,7	.	20
Zannichellia palustris ssp. *palustris*	*	63	40,0	.	0,0
Cardamine amara	*	.	0,0	58	33,3
Lemna minor	***	.	13,3	83	80,0
Myosotis scorpioides scorpioides	**	.	0,0	68	46,7
Ranunculus repens	**	.	33,3	78	80,0
Ranunculus sceleratus	*	.	6,7	58	33,3
Spirodela polyrhiza	*	.	0,0	58	33,3
Moose					
Bryum bimum	**	68	46,7	.	0,0
Bryum spp.	*	58	33,3	.	0,0
Cratoneuron filicinum	*	64	46,7	.	6,7
Fissidens adianthoides	*	63	46,7	.	0,0
Pellia endiviifolia	**	68	46,7	.	0,0
Brachythecium rutabulum	*	.	6,7	64	46,7
Eurhynchium hians	*	.	0,0	58	33,3
Plagiomnium undulatum	*	.	0,0	63	40,0
Armleuchteralgen					
Chara contraria	*	58	33,3	.	0,0
Chara globularis	**	73	60,0	.	0,0
Chara vulgaris	***	97	100,0	.	0,0

Der wichtigste Faktor, der die Artenvielfalt an den Gewässern förderte war die Sonnenscheindauer (Tab. 3). Bei allen sieben betrachteten Pflanzengruppen bestand ein positiver Zusammenhang zwischen Sonnenscheindauer und Artenvielfalt. Die Strukturvielfalt des Gewässers (‚Diversität Gewässer‘) hatte darüber hinaus einen positiven Einfluss auf die Vielfalt aller Arten, aller Gefäßpflanzenarten, aller Moosarten und gefährdeter Moosarten. Zudem hatten die Strukturvielfalt des Gewässerufers (‚Diversität Ufer‘; alle Moosarten) und der Anteil der Amphibischen Zone (Armleuchteralgen) einen positiven Einfluss auf die Artenvielfalt.

Tab. 3: Multivariable Modelle: Einfluss der Umweltparameter (Prädiktorvariablen) auf die Anzahl aller Arten (a), gefährdeter Arten (b), Gefäßpflanzenarten (c), Armleuchteralgenarten (d), Moosarten (e), gefährdeter Gefäßpflanzenarten (f) und gefährdeter Moosarten (g) in Steinbruch- und Kontrollgewässern (*N* = 30). Der Einfluss der Variablen wurde mittels generalisierter linearer gemischter Modelle (GLMM; Fehlerstruktur: negativ-binomial) mit ‘Teiluntersuchungsgebiet’ als Zufallsfaktor analysiert. R^2_m = durch feste Effekte erklärte Varianz, R^2_c = durch Zufallseffekte erklärte Varianz (Nakagawa et al. 2017). rP = Relative Parameterbedeutung. Statistische Unterschiede sind folgendermaßen angegeben: n.s. = nicht signifikant; $P \geq 0{,}05$; * $P < 0{,}05$; ** $P < 0{,}01$; *** $P < 0{,}001$.

Parameter	Estimate	Standardfehler	*Z*	rP	*P*
a) Alle Arten (R^2m = 0,48, R^2c = 0,48)					
(Intercept)	2,04	0,26	7,89	.	***
Diversität Gewässer	$9{,}52 \times 10^{-2}$	$2{,}93 \times 10^{-2}$	3,25	1,00	**
Sonnenschein	$3{,}61 \times 10^{-2}$	$1{,}32 \times 10^{-2}$	2,73	1,00	**
b) Gefährdete Arten (R^2_m = 0,39–0,48, R^2_c = 0,39–0,48)					
(Intercept)	–1,39	0,71	1,89	.	n.s.
Sonnenschein	$1{,}21 \times 10^{-1}$	$3{,}40 \times 10^{-2}$	3,37	1,00	***
c) Alle Gefäßpflanzenarten (R^2_m = 0,25–0,35, R^2_c = 0,25–0,35)					
(Intercept)	2,09	0,34	5,88	.	***
Diversität Gewässer	$9{,}24 \times 10^{-2}$	$3{,}39 \times 10^{-2}$	2,60	0,84	**
Sonnenschein	$3{,}47 \times 10^{-2}$	$1{,}64 \times 10^{-2}$	2,02	0,70	*
d) Gefährdete Gefäßpflanzenarten (R^2_m = 0,38, R^2_c = 0,47)					
(Intercept)	-0,72	0,53	1,31	.	n.s.
Sonnenschein	$8{,}14 \times 10^{-2}$	$3{,}56 \times 10^{-2}$	2,17	0,78	*
e) Alle Moosarten (R^2_m = 0,38–0,54, R^2_c = 0,47–0,54)					
(Intercept)	–0,24	0,57	0,40	.	n.s.
Diversität Ufer	$3{,}79 \times 10^{-1}$	$1{,}77 \times 10^{-1}$	2,05	0,94	*
Sonnenschein	$5{,}18 \times 10^{-2}$	$2{,}23 \times 10^{-2}$	2,23	0,69	*
Diversität Gewässer	$1{,}38 \times 10^{-1}$	$5{,}75 \times 10^{-2}$	2,31	0,56	*
f) Gefährdete Moosarten (R^2_m = 0,59–0,81, R^2_c = 0,59–0,81)					
(Intercept)	–8,72	2,88	2,91	.	**
Diversität Gewässer	$3{,}76 \times 10^{-1}$	$1{,}46 \times 10^{-1}$	2,44	1,00	*
Sonnenschein	$3{,}84 \times 10^{-1}$	$1{,}43 \times 10^{-1}$	2,57	0,93	*
g) Alle Armleuchteralgenarten (R^2_m = 0,51–0,64, R^2_c = 0,51–0,64)					
(Intercept)	–3,88	1,25	2,97	.	**
Sonnenschein	$2{,}50 \times 10^{-1}$	$7{,}04 \times 10^{-2}$	3,37	1,00	***
Amphibische Zone	$1{,}80 \times 10^{-2}$	$8{,}03 \times 10^{-3}$	2,13	0,82	*

4 Amphibien – Vergleich der Zönosen von Kleingewässern in Steinbrüchen und in der Normallandschaft

4.1 Material und Methoden

Untersuchungsgebiet: Westfälische Bucht und Ostwestfalen (siehe auch Kettermann & Fartmann in Überarbeitung; Anhang I).

Versuchsdesign: Vergleich von 15 Kleingewässern in Steinbrüchen mit 15 Kleingewässern in der Normallandschaft; vier Erfassungstermine Anfang März und Anfang Mai (siehe auch Kettermann & Fartmann in Überarbeitung; Anhang I).

4.2 Ergebnisse

Umweltbedingungen

Die Habitat- und Landschaftsqualität unterschieden sich deutlich zwischen Steinbruch- und Kontrollgewässern (Tab. 4). Bei Steinbruchgewässern machte die amphibische Zone vier Fünftel des Gewässers aus, ihr Anteil war damit mehr als doppelt so hoch wie bei den Kontrollgewässern. Am Ufer waren darüber hinaus die Sonnenscheindauer (Frühjahr und Sommer) höher, die Baumdeckung geringer, der Anteil an Offenboden höher und die Krautschicht hochwüchsiger an Steinbruchgewässern als an den Kontrollen. Die beiden Gewässertypen unterschieden sich auch deutlich in der Besiedlung durch Fische (Tab. 5). Steinbruchgewässer waren bis auf eine Ausnahme nie von Fischen besiedelt. Im Gegensatz dazu wies fast die Hälfte der Kontrollgewässer Fischvorkommen auf. Die deutlichen Unterschiede in den Umweltbedingungen zeigt auch der Biplot der Hauptkomponentenanalyse (Abb. 3). Entlang der ersten Achse sind Steinbruch- und Kontrollgewässer klar voneinander getrennt. Insbesondere eine höhere Ufervegetation ist charakteristisch für die Kontrollgewässer, während eine ausgedehntere amphibische Zone, eine längere Sonnenscheindauer und mehr Offenboden typisch für Steinbruchgewässer sind.

Amphibienzönosen in Abhängigkeit von den Umweltbedingungen

Insgesamt haben wir 12 Amphibienarten nachgewiesen, darunter waren fünf gefährdete Arten: Geburtshelferkröte (*Alytes obstetricans*), Kammmolch (*Triturus cristatus*), Kleiner Wassserfrosch (*Pelophylax lessonae*), Kreuzkröte (*Epidalea calamita*) und Laubfrosch (*Hyla arborea*) (Abb. 4). Drei Arten, *A. obstetricans*, *T. cristatus* und Teichmolch (*Lissotriton vulgaris*), wiesen in Steinbruchgewässern eine höhere Stetigkeit auf und drei Arten, *A. obstetricans*, *E. calamita* und Feuersalamander (*Salamandra salamandra*), wurden ausschließlich in Steinbruchgewässern nachgewiesen. Zudem waren die Anzahl aller Arten, die Anzahl gefährdeter Arten und die Molchabundanzen in Steinbruchgewässern höher als in Kontrollgewässern (Abb. 5).

In den GLMM-Analysen wurde die Artenzusammensetzung in den Gewässern ausschließlich durch die Habitatqualität bestimmt, genauer gesagt durch den Anteil der amphibischen Zone und die Sonnenscheindauer im Frühjahr (Tab. 6, Abb. 6). Die Anzahl aller Arten und die Molchabundanzen wurden durch eine ausgedehntere amphibische Zone gefördert, die Anzahl gefährdeter Arten dagegen durch eine längere Besonnung.

Tab. 4: Übersicht über die Umweltparameter (arithm. Mittel [Ø] ± Standardfehler [SF], Minimum und Maximum) in Steinbruchgewässern (Steinbruch, *N* = 15) und Kontrollgewässern (Kontrolle, *N* = 15). Unterschiede zwischen den beiden Gewässertypen wurden mittels generalisierter linearer gemischter Modelle (GLMM; Fehlerstruktur: negativ-binomial für Zähldaten, proportional-binomial für Deckungen) mit 'Teiluntersuchungsgebiet' als Zufallsfaktor analysiert. Statistische Unterschiede sind folgendermaßen angegeben: n.s. = nicht signifikant; *P* ≥ 0,05; * *P* < 0,05; ** *P* < 0,01; *** *P* < 0,001.

Parameter	**Steinbruch**		**Kontrolle**		***P***
	Ø ± SF	Min.–Max.	Ø ± SF	Min.–Max.	
Habitatqualität					
Gewässergröße [m^2][1]	1.443 ± 394	73–5.811	867 ± 161	106–1.763	n.s.
pH[2]	7,6 ± 0,1	7,1–8,0	7,4 ± 0,1	7,1–8,0	n.s.
Leitfähigkeit [µS/cm][2]	436 ± 136	261–682	528 ± 52	255–918	n.s.
Sonnenschein Frühjahr [h/Tag][3]	10,4 ± 0,5	6–12	8,1 ± 0,7	4–13	**
Sonnenschein Sommer [h/Tag][3]	12,8 ± 0,5	9–15	6,8 ± 1,1	2–14	***
Deckung amphibische Zone [%]	80,0 ± 5,2	30–100	37,6 ± 9,1	10–100	***
Deckung Ufer [%]					
Bäume	2,3 ± 0,8	0–10	23,0 ± 6,0	0–65	**
Sträucher	16,8 ± 3,2	2,5–45,0	14,3 ± 4,0	0–40	n.s.
Feldschicht	16,0 ± 2,6	2,5–35,0	22,3 ± 4,7	5–60	n.s.
Streu	39,3 ± 4,4	5–65	40,0 ± 2,9	20–60	n.s.
Offenboden	30,0 ± 6,9	0–90	3,2 ± 1,1	0–15	***
Vegetationshöhe Ufer [cm]	32,7 ± 3,0	19–58	50,1 ± 5,4	20–102	**
Deckung Unterwasservegetation [%]	29,3 ± 6,4	0–80	20,7 ± 5,0	0–50	n.s.
Landschaftsqualität					
Meereshöhe [m NN][4]	167 ± 13	98–273	147 ± 14	91–259	n.s.
Jahresmitteltemperatur [°C][5]	9,3 ± 0,1	8,8–9,8	9,4 ± 0,1	8,5–9,9	n.s.
Gewässerkonnektivität [m][6]	789 ± 222	39–2479	481 ± 115	29–1.306	n.s.

[1] Berechnet anhand von Luftbildern in ArcGIS 10.3.1.

[2] Ermittelt mit einer Messsonde (Hanna HI 98129).

[3] Ermittelt mit einem Horizontoskop; arithmetisches Mittel der Messwerte im N, E, S und W des Gewässers (Holtmann et al. 2017).

[4] Die Meereshöhe wurde anhand topgraphischer Karten bestimmt.

[5] Langjähriges Mittel (1981–2010) basierend auf Rasterdaten (1 km^2) des Deutschen Wetterdiensts.

[6] Geometrisches Mittel der Entfernung zu dne nächsten drei Stillgewässern.

Tab. 5: Absolute und relative Häufigkeit der kategorialen Variable 'Fischvorkommen' in Steinbruch- und Kontrollgewässern. Unterschiede in absoluten Häufigkeiten zwischen den zwei Gewässertypen wurden mittels Fisher's-Exakt-Test analysiert. * *P* <0,05.

Parameter	**Steinbruch**		**Kontrolle**		***P***
	N	%	*N*	%	
Fisch					*
Präsenz	1	12,5	7	87,5	
Absenz	14	63,6	8	36,4	

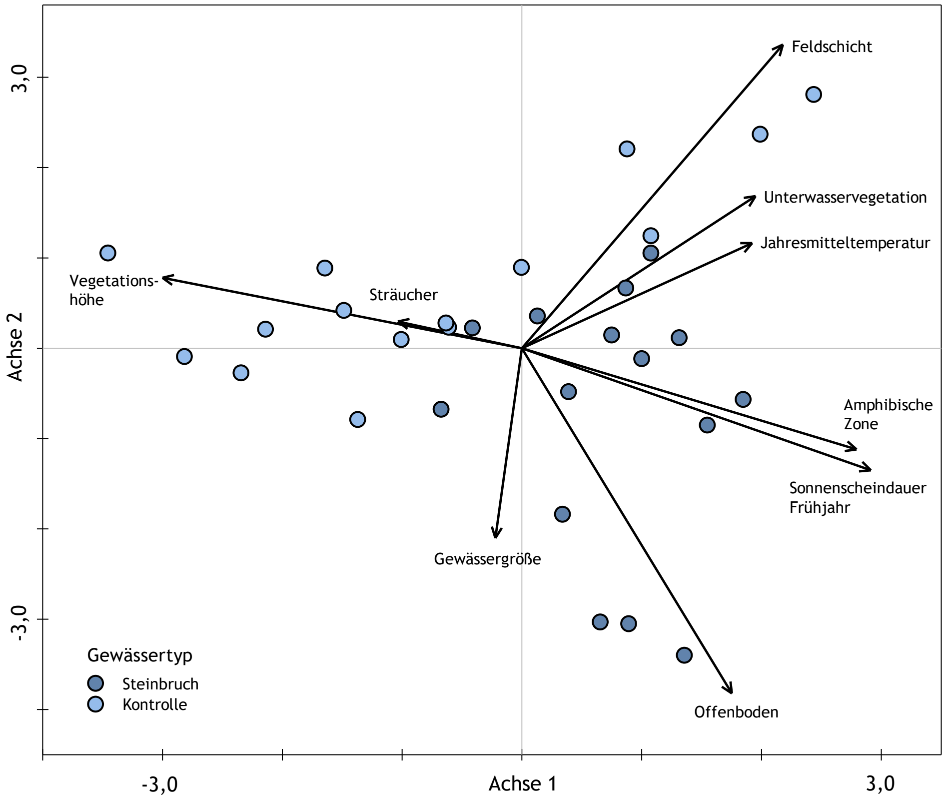

Abb. 3: Hauptkomponentenanalyse: Biplot basierende auf den beiden Gewässertypen und den erfassten Umweltparametern.

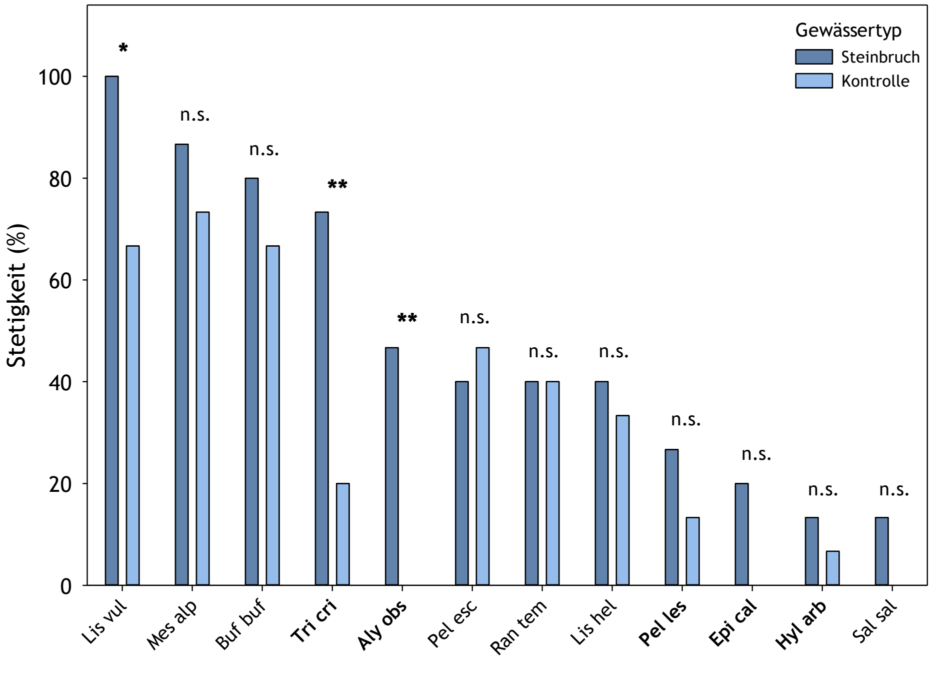

Abb. 4: Stetigkeit der Amphibien in Steinbruchgewässern (Steinbruch, *N* = 15) und Kontrollgewässern (Kontrolle, *N* = 15). Unterschiede in absoluten Häufigkeiten wurden mittels Chi²-Test getested. Abkürzungen: Lis vul = *Lissotriton vulgaris*, Mes alp = *Mesotriton alpestris*, Buf buf = *Bufo bufo*, Tri cri = *Triturus cristatus*, Aly obs = *Alytes obstetricans*, Pel esc = *Pelophylax* kl. *esculentus*, Ran tem = *Rana temporaria*, Lis hel = *Lissotriton helveticus*, Pel les = *Pelophylax lessonae*, Epi cal = *Epidalea calamita*, Hyl arb = *Hyla arborea*, Sal sal = *Salamandra salamandra*. Gefährdete Arten (LANUV 2011) sind durch Fettdruck hervorgehoben. n.s. = nicht signifikant; * *P* <0,05; ** *P* <0,01.

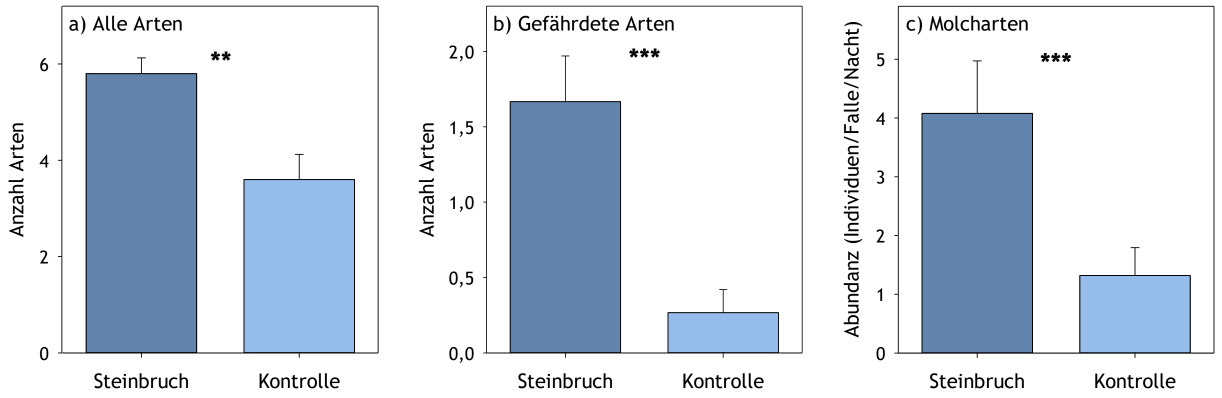

Abb. 5: Arithmethisches Mittel ± Standardfehler (SF) der Anzahl aller Arten (a), gefährdeter Arten (b) und Molchabundanz (c) in Steinbruchgewässern (Steinbruch, *N* = 15) und Kontrollgewässern (Kontrolle, *N* = 15). Unterschiede zwischen den beiden Gewässertypen wurden mittels generalisierter linearer gemischter Modelle (GLMM; Fehlerstruktur: Poisson) mit 'Teiluntersuchungsgebiet' als Zufallsfaktor analysiert. Statistische Unterschiede sind folgendermaßen angegeben: ** *P* < 0,01; *** *P* < 0,001.

Tab. 6: Multivariable Modelle: Einfluss der Umweltparameter (Prädiktorvariablen) auf die Anzahl aller Arten (a), gefährdeter Arten (b) und Molchabundanz (c) in Steinbruchgewässern (Steinbruch, *N* = 15) und Kontrollgewässern (Kontrolle, *N* = 15). Der Einfluss der Variablen wurde mittels generalisierter linearer gemischter Modelle (GLMM; Fehlerstruktur: Poisson) mit 'Teiluntersuchungsgebiet' als Zufallsfaktor analysiert. R^2_m = durch feste Effekte erklärte Varianz, R^2_c = durch Zufallseffekte erklärte Varianz (Nakagawa et al. 2017). rP = Relative Parameterbedeutung. Statistische Unterschiede sind folgendermaßen angegeben: n.s. = nicht signifikant; *P* ≥ 0,05; * *P* < 0,05; ** *P* < 0,01; *** *P* < 0,001.

Parameter	**Estimate**	**Standardfehler**	***Z***	**rP**	***P***
a) Anzahl aller Arten (R^2m = 0,12, R^2c =0,12)					
(Intercept)	1,23	0,18	6,69	.	***
Amphibische Zone	$5{,}04 \times 10^{-3}$	$2{,}52 \times 10^{-3}$	2,00	1,00	*
b) Anzahl gefährdeter Arten (R^2_m = 0,12–0,30, R^2_c=0,23–0,30)					
(Intercept)	−2,51	1,37	1,77	.	n.s.
Sonnenschein Frühjahr	$2{,}36 \times 10^{-1}$	$1{,}08 \times 10^{-2}$	2,08	0,79	*
Amphibische Zone	$1{,}31 \times 10^{-3}$	$6{,}94 \times 10^{-3}$	1,80	0,66	n.s.
c) Molchabundanz (R^2_m = 0,32–0,36, R^2_c=0,98)					
(Intercept)	−0,08	0,70	0,11	.	n.s.
Amphibische Zone	$2{,}70 \times 10^{-2}$	$9{,}23 \times 10^{-3}$	2,77	1,00	**
Offenboden	$1{,}82 \times 10^{-2}$	$1{,}42 \times 10^{-2}$	1,22	0,29	n.s.

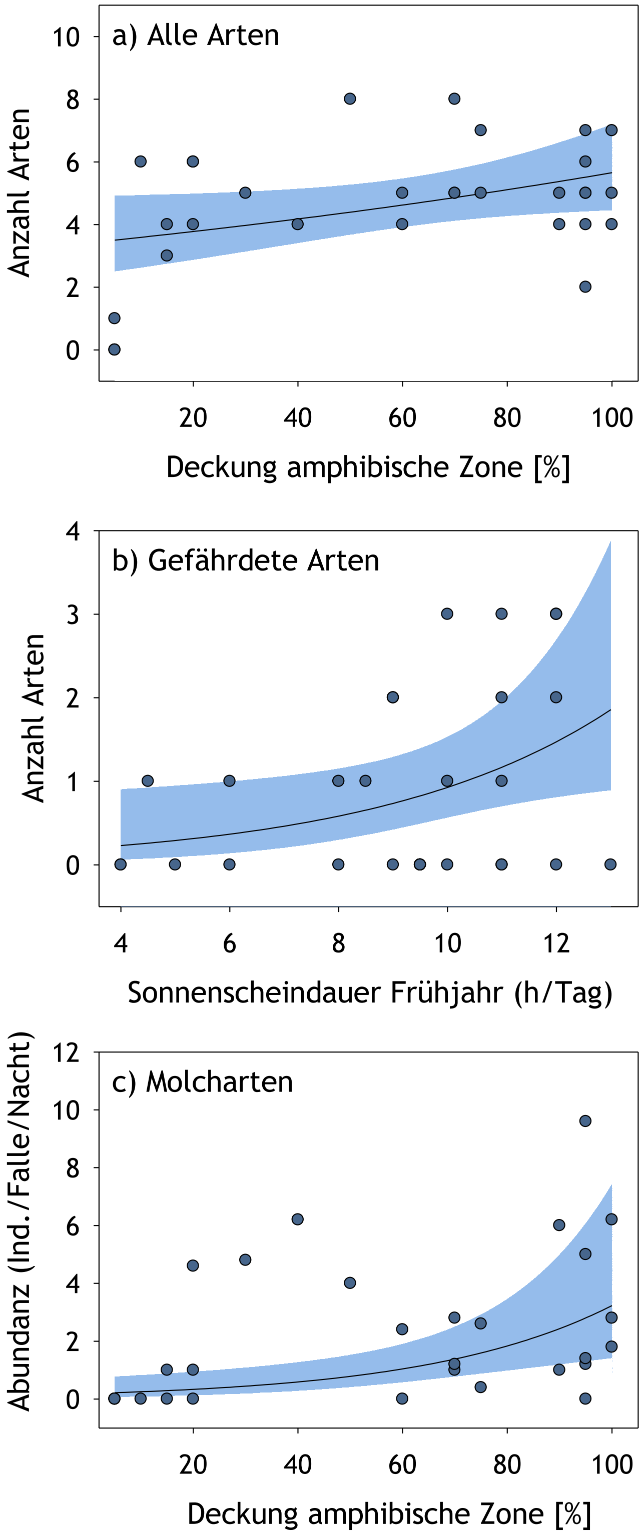

Abb. 6: Zusammenhang zwischen der Anzahl aller Arten (a), gefährdeter Arten (b) und Molchabundanz (c) und signifikanten Umweltparametern der multivariable Modelle (*N* = 30). Bezüglich der statistischen Kennwerte s. Tab. 6. (a) y = 0,005038 + 1,228947 × (amphibische Zone), $P < 0{,}05$, $R^2_m = 0{,}12$, $R^2_c = 0{,}12$; (b) y = 0,02316 + (–2,39122) × (Sonnenscheindauer Frühjahr), $P < 0{,}05$, $R^2_m = 0{,}16$, $R^2_c = 0{,}23$; (c) y = 0,028269 + (–0,044221) × (amphibische Zone), $P < 0{,}01$, $R^2_m = 0{,}32$, $R^2_c = 0{,}98$. R^2_m = durch feste Effekte erklärte Varianz, R^2_c = durch Zufallseffekte erklärte Varianz (Nakagawa et al. 2017). Ind. = Individuen. Blaue Schraffur: 95-%-Konfidenzintervall.

5 Tagfalter – Habitatpräferenzen des Argus-Bläulings (*Plebejus argus*) in Kalksteinbrüchen und Kalkmagerrasen

5.1 Material und Methoden

Untersuchungsgebiet: Diemeltal (siehe auch Münsch & Fartmann 2022; Anhang I)

Versuchsdesign: Vergleich von 51 Kalksteinbrüchen und 99 Kalkmagerrasen; zwei Erfassungstermine Mitte Juni bis Anfang Juli (siehe auch Münsch & Fartmann 2022; Anhang I).

5.2 Ergebnisse

Verbreitung im Untersuchungsgebiet

Insgesamt waren 29 (19 %) der 150 untersuchten Flächen vom Argus-Bläuling (*Plebejus argus*) besiedelt und 22 (15%) zählten zu den ehemals, nun aber nicht mehr besiedelten Flächen. Für alle anderen 99 (66%) Flächen, die aktuell nicht besiedelt waren lagen keine Angaben zu historischen Vorkommen vor. Insgesamt war die Stetigkeit von *P. argus* in Steinbrüchen (n = 21, 41 % aller untersuchten Steinbrüche) fünfmal so hoch wie in den Magerrasen (n = 8, 8 % aller untersuchten Magerrasen). Die absolute Häufigkeit von aktuell und ehemals besiedelten Flächen unterschied sich ebenfalls zwischen Steinbrüchen und Magerrasen (Tab. 7): In den Steinbrüchen war das Verhältnis etwa 3 : 1, in den Magerrasen dagegen 1 : 2. Zudem hatte das Management der Steinbrüche und Magerrasen einen starken Einfluss auf das Vorkommen von *P. argus*. Alle aktuell noch im Abbau befindlichen Steinbrüche waren besiedelt, während die Art bereits aus zwei Fünftel der nicht mehr betriebenen Steinbrüche verschwunden war. In brachliegenden Magerrasen kam die Art gar nicht mehr vor und selbst in zwei Fünftel der früher besiedelten und immer noch bewirtschafteten Magerrasen war *P. argus* bereits verschwunden.

Tab. 7: Absolute und relative Häufigkeit der Besiedlung von Kalksesteinbruchen und Kalkmagerrasen durch den Argus-Bläuling (*Plebejus argus*) in Abhängikeit von den kategorialen Variablen ‘Habitattyp’ und ‘Landnutzung’. Unterschiede in absoluten Häufigkeiten zwischen besiedelten und nicht mehr besiedelten Habitaten wurden mittels Fisher’s-Exakt-Test analysiert. * *P* <0.05.

Parameter	**Besiedelt (*N* = 29)**		**Nicht besiedelt (*N* = 22)**		***P***
	N	%	*N*	%	
Habitattyp					*
Steinbruch	21	72,4	8	27,6	
Magerrasen	8	36,4	14	63,6	
Landnutzung					
Steinbruch					*
In Betrieb	9	100,0	0	0,0	
Außer Betrieb	12	60,0	8	40,0	
Magerrasen					*
Genutzt	8	57,1	6	42,9	
Brachliegend	0	0,0	8	100,0	

Mit Ausnahme der Flächengröße, unterschieden sich alle metrischen Variablen zwischen den vier Habitattypen (Tab. 8, Abb. 7). Insbesondere aktuell besiedelte Flächen unterschieden sich stark von ehemals besiedelten Flächen. Darüber hinaus waren aktuell besiedelte Steinbrüche durch besonders extreme Umweltbedingungen gekennzeichnet. Alle makroklimatischen Parameter waren stark interkorreliert (Tab. 8). Aktuell besiedelte Steinbrüche befanden sich in den höchsten Lagen des Untersuchungsgebiets und waren entsprechend durch die meisten Frosttage und höchsten Niederschläge, aber geringsten Temperaturen gekennzeichnet. Aktuell besiedelte Steinbrüche unterschieden sich deutlich in den Umweltbedingungen von ehemals besiedelten Steinbrüchen. Besiedelte Magerrasen wiesen oft intermediäre Umweltbedingungen zwischen den beiden Steinbruchtypen auf. Besiedelte Steinbrüche waren durch die höchste Habitatkonnektivität gekennzeichnet und differierten von ehemals besiedelten Flächen. Im Gegensatz dazu gab es keine Unterschiede zwischen aktuell besiedelten Magerrasen und den drei anderen Habitattypen hinsichtlich des Makroklimas und der Landschaftsqualität.

Die Habitatqualitätsparameter waren ebenfalls stark interkorreliert (Tab. 8). In aller Regel bestand ein Gradient von aktuell besiedelten Steinbrüchen über aktuell besiedelte Magerrasen zu ehemals besiedelten Flächen. Entlang dieses Gradienten nahmen die Vegetationsdichte und -höhe, die Deckung von kleinen Sträuchern, Gras, Moosen und Streu sowie die Bodengründigkeit zu. Im Gegensatz dazu, nahmen die Deckung des Offenbodens, Bodenskeletts und der Wirtspflanze *Lotus corniculatus* ab. Die Sonnenscheindauer war am geringsten in ehemals besiedelten Steinbrüchen und unterschied sich damit von den drei anderen Habitattypen.

Aufgrund der starken Unterschiede in der Vegetationsstruktur zwischen den Habitattypen galt dies auch für das Mikroklima (Abb. 7). Am Tage nahmen die Temperaturen von aktuell besiedelten Steinbrüchen über ehemals besiedelte Magerrasen zu ehemals besiedelten Steinbrüchen ab. Aktuell besiedelte Magerrasen vermittelten zwischen den beiden erstgenannten Habitattypen. Nachts waren die Muster ähnlich, allerdings unterschieden sich nur aktuell besiedelte von ehemals besiedelten Steinbrüchen.

In den GLMM-Analysen wurden das Makroklima, die Landschaftsqualität und die Habitatqualität als Schlüsselfaktoren für das Vorkommen von *P. argus* identifiziert (Tab. 9). Im Makroklimamodell nahm die Vorkommenswahrscheinlichkeit mit der Temperatur zu. Im Landschaftsqualitätsmodell bestand ein positiver Zusammenhang zwischen Konnektivität und dem Vorkommen von *P. argus*. Im Habitatqualitätsmodell stieg die Vorkommenswahrscheinlichkeit mit der Deckung der Wirtspflanze, *L. corniculatus*. Im Synthesemodell war dies schließlich die einzige erklärende Variable (Tab. 9, Abb. 8). Die Modellgüte war in allen Modellen sehr hoch (R^2_m 0.35–0.87, *AUC* 0.89–0.97).

Abundanzen

Die mittleren Abundanzen der Imagines von *P. argus* waren in besiedelten Steinbrüchen fast vier Mal so hoch wie in besiedelten Magerrasen (Abb. 9). In den GLMM-Analysen war die Habitatqualität der Schlüsselfaktor für hohe Falterdichten (Tab. 10). Das Makroklima und die Landschaftsqualität hatten dagegen keinen Einfluss. Die Abundanzen von *P. argus* nahmen mit der Deckung der Deckung der Wirtspflanze, *L. corniculatus*, der Deckung des Bodenskeletts und eine abnehmenden Vegetationsdichte zu (Habitatqualitäts- und Synthesemodell; Tab. 10, Abb. 10). Die Modellgüte war wieder sehr hoch (R^2_m 0.37–0.41).

Tab. 8: Übersicht über die Umweltparameter (arithm. Mittel [Ø] ± Standardfehler [SF]) in aktuell besiedelten und ehemals besiedelten Habitaten. Unterschiede zwischen den Habitattypen wurden mittels (generalisierter) linearer gemischter Modelle (GLMM/LMM) mit 'Teiluntersuchungsgebiet' als Zufallsfaktor und Tukey-Test als Post-hoc-Test analysiert. Statistische Unterschiede sind folgendermaßen angegeben: n.s. = nicht signifikant; $P \geq 0,05$; * $P < 0,05$; ** $P < 0,01$; *** $P < 0,001$. Unterschiedliche Buchstaben kennzeichnen signifikante Unterschiede zwischen den Habitattypen ($P < 0,05$).

Parameter	**Besiedelt (*n* = 29)**		**Ehemals besiedelt (*n* = 22)**		***P***	***r***	**Verw. Variable**
	Steinbruch (*n* = 21)	Magerrasen (*n* = 8)	Steinbruch (*n* = 8)	Magerrasen (*n* = 14)			
Makroklima							
Meereshöhe [m NN]	380,8 ± 17,7^{a}	314,1 ± 39,8^{ab}	252,9 ± 21,0^{b}	221,5 ± 10,4^{b}	***	–0,82	▶ Temperatur
Frosttage^{a}	80,2 ± 1,4^{a}	77,4 ± 1,9^{ab}	74,4 ± 1,6^{b}	72,7 ± 0,8^{b}	***	–0,86	
Niederschlag [mm]^{b}	746,8 ± 20,4^{a}	730,4 ± 34,3^{ab}	653,3 ± 11,8^{b}	658,0 ± 7,6^{b}	**	–0,83	
Temperatur [°C]^{c}	9,1 ± 0,1^{a}	9,3 ± 0,2^{ab}	9,6 ± 0,1^{b}	9,7 ± 0,1^{b}	***	1,00	
Landschaftsqualität							
Flächengröße [ha]	1,0 ± 0,1	0,8 ± 0,2	1,4 ± 0,2	2,7 ± 0,7	n.s.		
Konnektivität [km]^{d}	1,8 ± 0,4^{a}	3,0 ± 0,5^{ab}	4,8 ± 0,6^{b}	6,1 ± 0,7^{b}	***		
Habitatqualität							
Sonnenschein [h/Tag]^{e}	13,4 ± 0,5^{a}	12,3 ± 0,7^{a}	10,4 ± 0,8^{b}	11,8 ± 0,5^{a}	**		
Vegetationstruktur							
Vegetationsdichte [%]							
0-5 cm	65,3 ± 2,7^{a}	71,0 ± 3,4^{ab}	86,7 ± 5,3^{bc}	94,6 ± 2,1^{c}	***	0,79	▶ Vegetationsdichte 10–15 cm
10-15 cm	27,9 ± 2,7^{a}	19,0 ± 2,1^{a}	49,2 ± 8,8^{b}	52,9 ± 6,6^{b}	***	1,00	
20-25 cm	5,0 ± 0,9^{ab}	2,3 ± 0,6^{a}	14,3 ± 5,7^{ab}	17,1 ± 5,5^{b}	*	0,84	
Vegetationshöhe [cm]	14,3 ± 1,0^{a}	11,5 ± 1,2^{a}	17,3 ± 2,1^{ab}	19,8 ± 2,3^{b}	*	0,81	
Deckung [%]							
Offenboden	11,0 ± 1,8^{ab}	21,7 ± 3,2^{a}	6,3 ± 1,2^{b}	4,9 ± 0,8^{b}	***		
Bodenskelett^{f}	20,3 ± 2,4^{a}	5,7 ± 1,6^{b}	5,0 ± 1,6^{b}	2,1 ± 0,8^{b}	***		
Sträucher [<0,5 m]	0,8 ± 0,3^{a}	0,9 ± 0,3^{ab}	2,8 ± 1,1^{ab}	3,7 ± 0,9^{b}	**		
Kräuter	51,7 ± 1,8^{a}	41,1 ± 2,9^{b}	49,3 ± 1,9^{ab}	41,6 ± 1,8^{b}	***		
Gräser	15,1 ± 1,9^{a}	30,0 ± 4,9^{b}	37,1 ± 3,7^{b}	51,2 ± 2,8^{c}	***	–0,83	▶ *L. corniculatus*
Lotus corniculatus	38,1 ± 2,6^{a}	24,2 ± 3,7^{b}	15,7 ± 3,3^{bc}	8,9 ± 1,2^{c}	***	1,00	
Moose	26,1 ± 3,4^{ab}	17,3 ± 4,1^{a}	36,5 ± 6,3^{b}	38,6 ± 5,3^{b}	*	–0,70	
Streu	4,5 ± 1,4^{a}	5,4 ± 2,7^{a}	30,4 ± 7,9^{b}	33,0 ± 6,0^{b}	***	–0,74	
Bodentiefe [cm]	5,3 ± 0,6^{a}	7,2 ± 0,9^{a}	10,4 ± 1,6^{ab}	18,7 ± 1,6^{b}	***	–0,73	

Tab. 9: Multivariable Modelle: Einfluss der Umweltparameter (Prädiktorvariablen) auf das Vorkommen des Argus-Bläulings (*Plebejus argus*) (aktuell besiedelte [*n* = 29] versus ehemals besiedelte Habitate [*n* = 22]). Der Einfluss der Variablen wurde mittels generalisierter linearer gemischter Modelle (GLMM; Fehlerstruktur: binomial) mit ‘Habitattyp’ und ‘Teiluntersuchungsgebiet’ als Zufallsfaktor analysiert. SF = Standardfehler. R^2_m = durch feste Effekte erklärte Varianz, R^2_c = durch Zufallseffekte erklärte Varianz (Nakagawa et al. 2017). *AUC* = Area under curve (Maß für die Modellgüte; Fielding & Bell 1997). Statistische Unterschiede sind folgendermaßen angegeben: n.s. = nicht signifikant; $P \geq 0{,}05$; * $P < 0{,}05$; ** $P < 0{,}01$.

Parameter	**Estimate**	**SF**	**Z**	***P***	R^2_m	R^2_c	**AUC**
a) Makroklimamodell					0,35	0,46	0,89
(Intercept)	34,52	12,60	2,74	*			
Temperatur	–3,63	1,33	–2,74	*			
b) Landschaftsqualitätsmodell					0,72–0,77	0,75–0,79	0,94
(Intercept)	6,53	2,64	2,42	*			
Konnektivität	0,85	0,30	2,78	**			
Nicht signifikant: Flächengröße							
c) Habitatqualitätsmodell					0,84–0,87	0,87–0,89	0,97
(Intercept)	–5,15	3,49	1,45	n.s.			
Lotus corniculatus	0,27	0,09	2,76	**			
Nicht signifikant: Bodenskelett, Kräuter, Offenboden, Sonnenschein, Sträucher, Vegetationsdichte							
d) Synthesemodell					0,80–0,83	0,82–0,85	0,96
(Intercept)	14,82	15,45	0,95	n.s.			
Lotus corniculatus	0,24	0,08	2,70	**			
Nicht signifikant: Temperatur, Konnektivität							

Tab. 10: Multivariable Modelle: Einfluss der Umweltparameter (Prädiktorvariablen) auf die Abundanzen des Argus-Bläulings (*Plebejus argus*) (*n* = 29). Der Einfluss der Variablen wurde mittels generalisierter linearer gemischter Modelle (GLMM; Fehlerstruktur: negativ-binomial) mit ‘Habitattyp’ und ‘Teiluntersuchungsgebiet’ als Zufallsfaktor analysiert. SF = Standardfehler. R^2_m = durch feste Effekte erklärte Varianz, R^2_c = durch Zufallseffekte erklärte Varianz (Nakagawa et al. 2017). Statistische Unterschiede sind folgendermaßen angegeben: n.s. = nicht signifikant; $P \geq 0{,}05$; * $P < 0{,}05$; ** $P < 0{,}01$.

Parameter	**Estimate**	**SF**	**Z**	***P***	R^2_m	R^2_c
a) Makroklimamodell						
Nicht signifikant: Temperatur						
b) Landschaftsqualitätsmodell						
Nicht signifikant: Flächengröße, Konnektivität						
c) Habitatqualitätsmodell					0,37–0,41	0,37–0,41
(Intercept)	0,34	0,52	0,65	n,s,		
Lotus corniculatus	0,03	0,01	3,06	**		
Bodenskelett	0,02	0,01	1,97	*		
Vegetationsdichte	–0,02	0,01	2,08	*		
Nicht signifikant: Kräuter, Offenboden, Sonnenschein, Sträucher, Vegetationshöhe						
d) Synthesemodell					0,37–0,41	0,37–0,41
(Intercept)	0,33	0,57	0,56	n,s,		
Lotus corniculatus	0,03	0,01	2,95	**		
Bodenskelett	0,02	0,01	2,08	*		
Vegetationsdichte	–0,01	0,01	2,09	*		

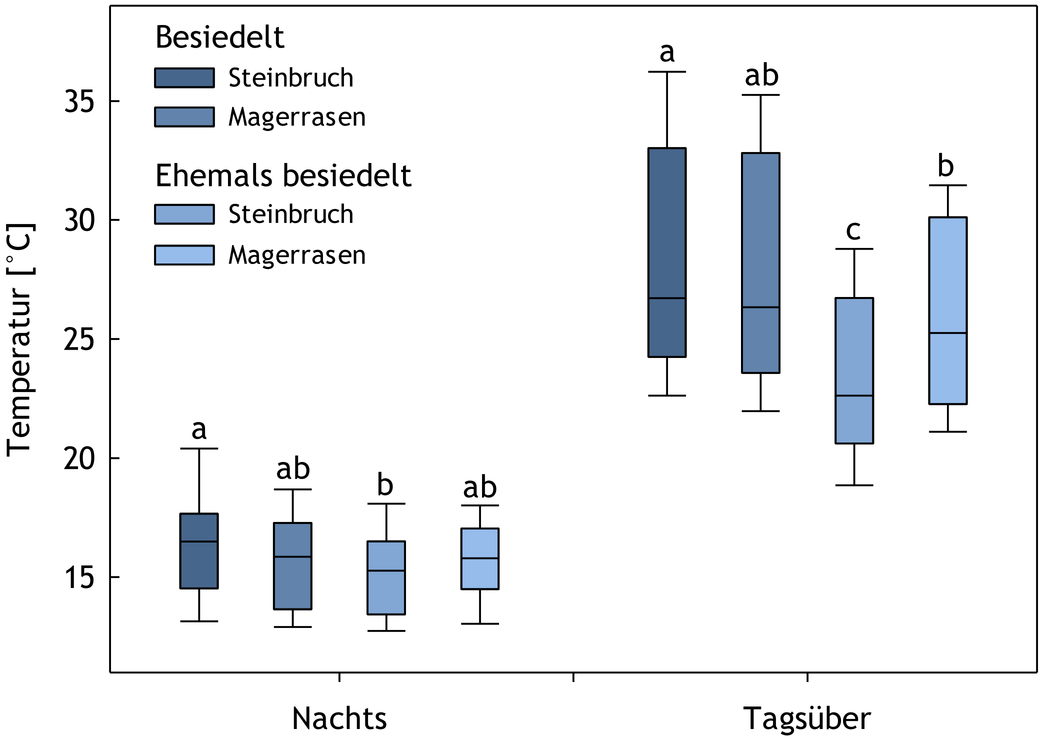

Abb. 7: Unterschiede in stündlichen Luftemperaturen in der Nacht (22:00 Uhr bis 07:00 Uhr) und am Tage (8:00 Uhr bis 21:00 Uhr) in den vier Habitatytpen. Messperiode: 23. Jul ibis 05. August 2019. Dartgestellt sind der Median, das 1. und 3. Quartil sowie das 10- und 90-%-Perzentil. Unterschiede zwischen den Habitattypen wuerden wurden mittels GLMM und nachfolgenden Tukey-Tests analysiert. Habitattypen ohme gemeinsame Buchstaben unetrscheiden sich significant ($P < 0,05$).

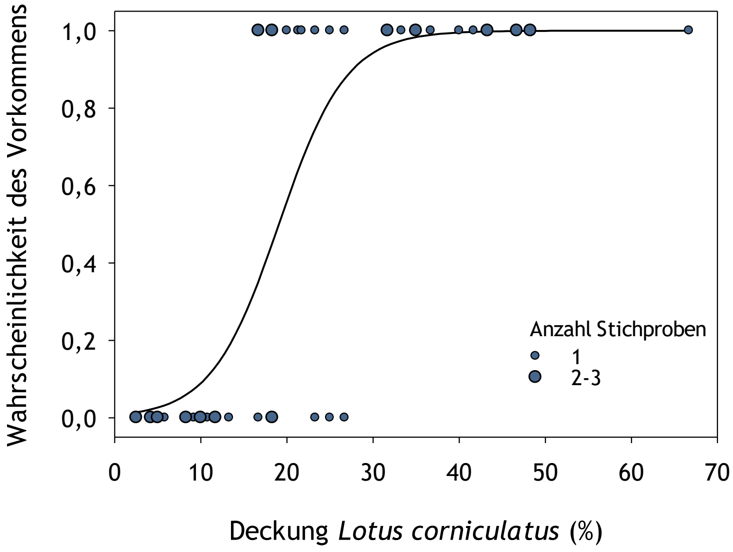

Abb. 8: Zusammenhang zwischen dem Vorkommen des Argus-Bläulings (*Plebejus argus*) und signifikanten Umweltparametern der multivariable Modelle (N = 51). Bezüglich der statistischen Kennwerte s. Tab. 9. y = 1 / (1 + exp (–(–4,87718 + 0,25596 × *L. corniculatus*))), P <0,01, R^2_m = 0,80, R^2_c = 0,80. R^2_m = durch feste Effekte erklärte Varianz, R^2_c = durch Zufallseffekte erklärte Varianz (Nakagawa et al. 2017). Blaue Schraffur: 95-%-Konfidenzintervall.

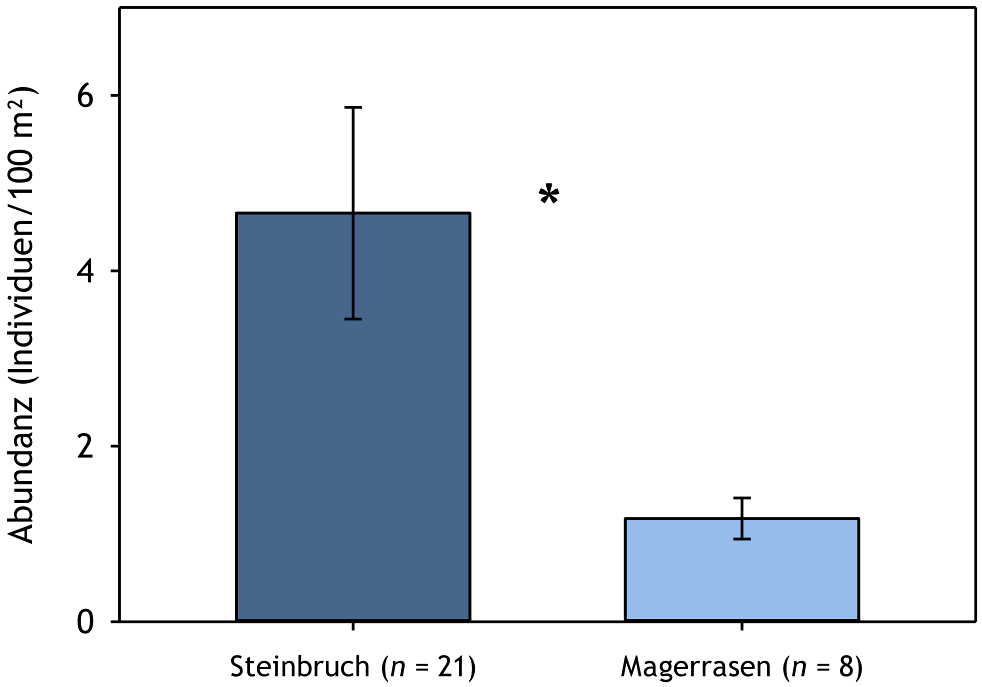

Abb. 9: Arithmethisches Mittel ± Standardfehler (SF) der Abundanz des Argus-Bläulings (*Plebejus argus*) in aktuelle besiedelten Kalksteinbrüchen und -Magerrasen. Unterschiede zwischen den beiden Gewässertypen wurden mittels generalisierter linearer gemischter Modelle (GLMM) mit ‘Teiluntersuchungsgebiet’ als Zufallsfaktor analysiert. Statistische Unterschiede sind folgendermaßen angegeben: * $P < 0,05$.

6 Wildbienen – Zönosen von Kalksteinbrüchen

6.1 Material und Methoden

Untersuchungsgebiet: Teutoburger Wald, Hellwegbörde, Lipperland und Weser-Leine-Bergland (siehe auch Kettermann et al. 2022; Anhang I)

Versuchsdesign: 16 Steinbrüche, davon 8 aktive und 8 stillgelegte; Transekterfassug; neun Erfassungstermine von März bis September (siehe auch Kettermann et al. 2022; Anhang I).

6.2 Ergebnisse

Umweltbedingungen

Weder das Makroklima noch die Landschaftsqualität unterschieden sich zwischen aktiven und stillgelegten Steinbrüchen (Tab. 11). Lediglich der Anteil an Siedlungs- und Verkehrsfläche war im Umfeld der aktiven Steinbrüche größer als in dem der stillgelegten Steinbrüche. Im Gegensatz dazu bestanden große Unterschiede in der Habitatqualität. Aktive Steinbrüche waren größer, wiesen mehr Pollenquellen und eine größere Ausdehnung früher Sukzessionsstadien (vegetationsfrei, ausdauernde Ruderalvegetation) auf, spätere Sukzessionsstadien (Kalkmagerrasen mit Gebüschen, Gebüsche und Wälder) nahmen dagegen kleinere Anteile ein als in stillgelegten Steinbrüchen. Alle anderen Parameter der Habitatqualität unterschieden sich nicht zwischen den beiden Steinbruchtypen. In stillgelegten Steinbrüchen lag die letzte Abbautätigkeit zwischen 12 bis 86 Jahre zurück (arith. Mittel ± Standardfehler: 39 ± 13 Jahre).

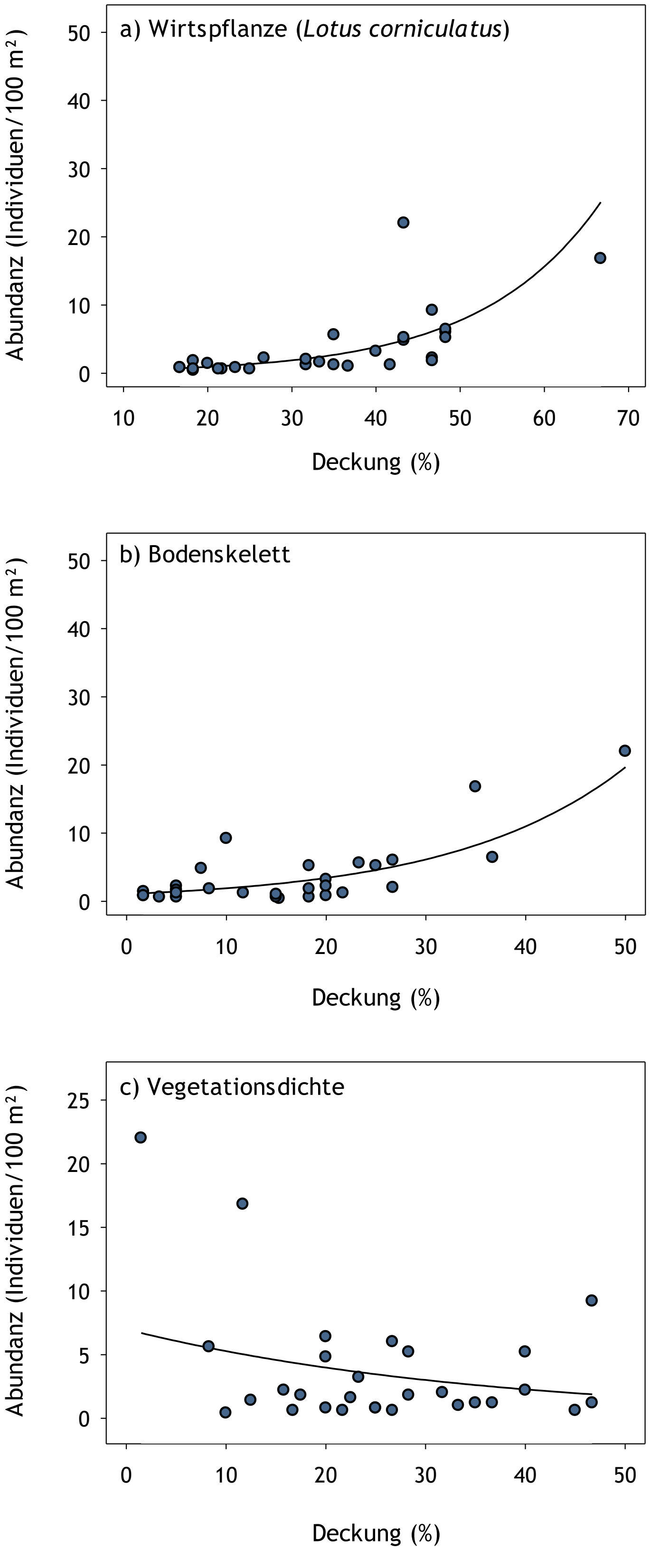

Abb. 10: Zusammenhang zwischen der Abundanz des Argus-Bläulings (*Plebejus argus*) und signifikanten Umweltparametern der multivariable Modelle ($N = 29$). Bezüglich der statistischen Kennwerte s. Tab. 10. a) y = exp (–1,47512 + 0,07043 × *L. corniculatus*), $P < 0{,}001$, $R^2_m = 0{,}60$, $R^2_c = 0{,}63$; b) y = exp (0,06747 + 0,05826 × Bodenskelett), $P < 0{,}01$, $R^2_m = 0{,}38$, $R^2_c = 0{,}40$; c) y = exp (1,94455 – 0,02811 × Vegetationsdichte), $P < 0{,}05$, $R^2_m = 0{,}14$, $R^2_c = 0{,}14$. R^2_m = durch feste Effekte erklärte Varianz, R^2_c = durch Zufallseffekte erklärte Varianz (Nakagawa et al. 2017). Blaue Schraffur: 95-%-Konfidenzintervall.

Bienenzönosen in Abhängigkeit von den Umweltbedingungen

Insgesamt haben wir 159 Bienenarten in den 16 Steinbrüchen nachgewisen (siehe Kettermann et al. 2022; Anhang I). Von diesen sind 44 (28 %) auf der Roten Liste Nordrhein-Westfalens enthalten und 35 (22%) zählen zu den oligolektischen Arten. Die Artenvielfalt aller, gefährdeter und oligolektischer Arten war jeweils in aktiven Steinbrüchen größer als in stillgelegten (Abb. 11).

Aktive Steinbrüche waren durch eine einzigartige Bienengemeinschaft gekennzeichnet. Anhand der Indikatorartenanalyse konnten für aktive Steinbrüche sechs charakterische Arten ermittelt werden, darunter eine gefährdete Art (*Osmia adunca*) (Tab. 12). Die stillgelegten Steinbrüche wiesen demgegenüber keine Indikatorarten auf.

Das Pollenangebot war der wichtigste Umweltfaktor, der die Artenvielfalt in den Steinbrüchen bestimmte (Tab. 13, Abb. 12). Die Anzahl aller, gefährdeter und oligolektischer Arten nahm mit der Vielfalt der Pollenquellen zu. Die Vielfalt der Pollenquellen war negativ mit der Deckung verbuschter Kalkmagerrasen und positiv mit der Deckung einjähriger Ruderalvegetation korreliert (siehe Kettermann et al. 2022; Anhang I).

Ausreichend Nisthabitate sind ebenfalls wichtig für artenreiche Bienenzönosen. Eine hohe Dichte an Abbruchkanten förderte die Artenvielfalt gefährdeter und oilgolektischer Arten Tab. 13, Abb. 12). Zuxdem nahm die Anzahl aller Arten mit der Deckung vegetationsfreier Bereiche zu. Dieser Parameter war negative mit der Deckung von Gebüschen korreliert (siehe Kettermann et al. 2022; Anhang I). Die Güte aller Modelle war sehr hoch (R^2_m = 0,64–0,90; R^2_c = 0,64–0,92).

In stillgelegten Steinbrüchen nahm die Artenvielfalt aller, gefährdeter und oligolektischer Bienen mit dem Umweltparameter 'Jahre seit Stilllegung' ab (Abb. 13). Die Variable war negativ mit der Anzahl der Pollenquellen und der Deckung einjähriger Ruderalvegetation korreliert (siehe Kettermann et al. 2022; Anhang I). Die Güte dieser Modelle war ebenfalls sehr hoch (R^2_m = 0,77–0,93; R^2_c = 0,87–0,93).

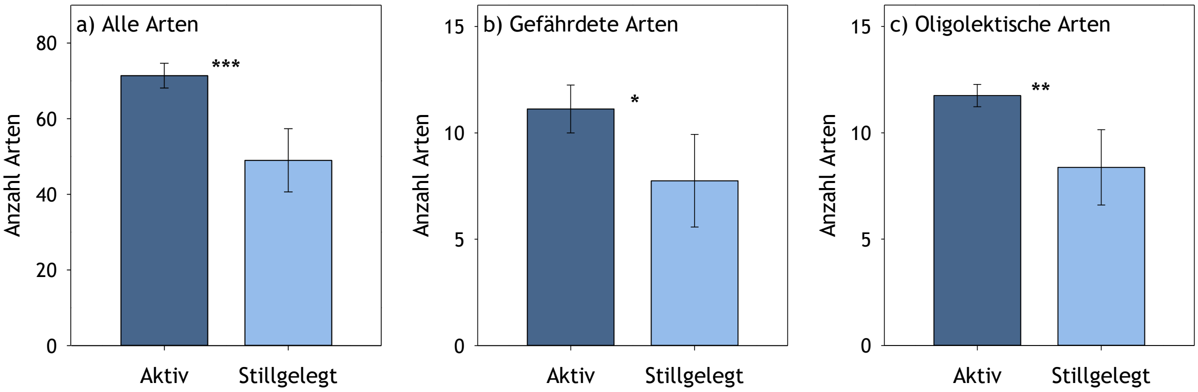

Abb. 11: Arithmethisches Mittel ± Standardfehler (SF) der Anzahl aller (a), gefährdeter (b) und oligolektischer Bienenarten (c) in aktiven (*N* = 8) und stillgelegten Kalksteinbrüchen (*N* = 8). Unterschiede zwischen den beiden Steinbruchtypen wurden mittels generalisierter linearer gemischter Modelle (GLMM; Fehlerstruktur: Poisson) mit 'Teiluntersuchungsgebiet' als Zufallsfaktor analysiert. Statistische Unterschiede sind folgendermaßen angegeben: * $P < 0,05$; ** $P < 0,01$; *** $P < 0,001$.

Tab. 11: Übersicht über die Umweltparameter (arithm. Mittel [Ø] ± Standardfehler [SF], Minimum und Maximum) in aktiven ($N = 8$) und stillgelegten Kalksteinbrüchen ($N = 8$). Unterschiede zwischen den beiden Steinbruchtypen wurden mittels generalisierter linearer gemischter Modelle (GLMM; Fehlerstruktur: Poisson) mit 'Teiluntersuchungsgebiet' als Zufallsfaktor analysiert. Statistische Unterschiede sind folgendermaßen angegeben: n.s. = nicht signifikant; $P \geq 0,05$; * $P < 0,05$; ** $P < 0,01$; *** $P < 0,001$.

Parameter	**Steinbruchtyp**				***P***
	Aktiv		**Stillgelegt**		
	Ø ± SF	Min.–Max.	Ø ± SF	Min. –Max.	
Makroklima					
Meereshöhe [m NN]	163 ± 21	108–289	208 ± 18	151–310	n.s.
Geographische Breite	8,7 ± 0,1	8–9	9,0 ± 0,1	9–9	n.s.
Mittlerer Jahresniederschlag [mm]	917 ± 29	830–1072	915 ± 35	815–1088	n.s.
Jahresmitteltemperatur [°C]	9,2 ± 0,2	8–10	9,1 ± 0,1	9–10	n.s.
Landschaftsqualität*					
Ackerland [%]	34,0 ± 8,0	11–67	27,1 ± 10,2	0–73	n.s.
Grünland [%]	10,4 ± 3,0	1–29	20,8 ± 8,2	0–75	n.s.
Wald [%]	34,1 ± 7,0	9–55	48,0 ± 8,7	18–88	n.s.
Siedlungs- und Verkehrsfläche [%]	15,9 ± 4,3	2–38	4,5 ± 3,7	0–30	*
Habitatqualität					
Habitattypen [%]					
Vegetationsfrei	29,3 ± 5,6	6–59	0,4 ± 0,4	0–3	***
Einjährige Ruderalvegetation	29,6 ± 4,5	15–57	24,5 ± 6,9	0–56	n.s.
Ausdauernde Ruderalvegetation	6,8 ± 2,4	1–21	1,0 ± 0,5	0–4	**
Frischgrünland	1,3 ± 0,6	0–4	2,1 ± 1,5	7–13	n.s.
Kalkmagerrasen mit Gebüschen	6,2 ± 1,7	2–17	10,1 ± 4,5	0–40	n.s.
Kalkmagerrasen ohne Gebüsche	4,0 ± 1,6	0–13	15,7 ± 3,9	7–40	**
Gebüsch	13,7 ± 2,1	7–23	22,2 ± 2,2	16–30	**
Saum	1,8 ± 0,5	0–4	2,1 ± 0,8	0–5	n.s.
Wald	4,2 ± 1,4	0–10	21,3 ± 6,0	0–55	**
Habitatheterogenität [Shannon-Index]	1,6 ± 0,1	1–2	1,5 ± 0,1	1–2	n.s.
Dichte Abbruchkanten [m/10ha]	1,6 ± 0,4	0,4–3,9	1,5 ± 0,4	0,0–3,3	n.s.
Pollenquellen [Anzahl Pflanzenarten]	68,0 ± 2,5	57–80	47,3 ± 6,5	17–64	***
Steinbruchgröße [ha]	52,6 ± 11,1	15–98	14,1 ± 4,2	6–35	**

* Deckung der Landnutzungstypen [%] innerhalb eines Radius von 200 m um den Steinbruch.

Tab. 12: Ergebnisse der Indikatorartenanalyse: Bienenindikatorarten in aktiven ($N = 8$) und stillgelegten Kalksteinbrüchen ($N = 8$). Es sind nur Arten mit einem signifikanten Indikatorwert (IW) dargestellt. Gefährdete Arten sind in Fettdruck hervorgehoben. % = Stetigkeit. Statistische Signifikanz ist folgendermaßen angegeben: * $P < 0,05$; ** $P < 0,01$.

Indikatorart	**Steinbruchtyp**				***P***
	Aktiv		Stillgelegt		
	IV	%	IV	%	
Andrena gravida	89	100,0	.	25,0	**
Hylaeus gredleri	88	87,5	.	12,5	**
Hylaeus signatus	85	100,0	.	37,5	*
Lasioglossum calceatum	85	100,0	.	37,5	*
Osmia adunca	80	75,0	.	12,5	*
Sphecodes geofrellus	80	75,0	,	12,5	*

Tab. 13: Multivariable Modelle: Einfluss der Umweltparameter (Prädiktorvariablen) auf die Anzahl aller (a), gefährdeter (b) und oligolektischer Bienenarten (c) in aktiven (*N* = 8) und stillgelegten Kalksteinbrüchen (*N* = 8). Der Einfluss der Variablen wurde mittels generalisierter linearer gemischter Modelle (GLMM; Fehlerstruktur: Poisson) mit 'Teiluntersuchungsgebiet' als Zufallsfaktor analysiert. SF = Standardfehler. R^2_m = durch feste Effekte erklärte Varianz, R^2_c = durch Zufallseffekte erklärte Varianz (Nakagawa et al. 2017). *rP* = Relative Parameterbedeutung. Statistische Unterschiede sind folgendermaßen angegeben: n.s. = nicht signifikant; $P \geq 0{,}05$; * $P < 0{,}05$; *** $P < 0{,}001$.

Parameter	**Estimate**	**SF**	**z**	***rP***	***P***
(a) Alle Arten (R^2_m = 0,83–0,90, R^2_c = 0,89–0,92)					
(Intercept)	2,78	0,23	11,00	.	***
Abbruchkanten	$4{,}41 \times 10^{-3}$	$1{,}02 \times 10^{-3}$	3,89	1,00	***
Pollenquellen	$1{,}57 \times 10^{-2}$	$3{,}92 \times 10^{-3}$	3,74	1,00	***
Vegetationsfrei	$5{,}55 \times 10^{-3}$	$2{,}17 \times 10^{-3}$	2,29	0,40	*
Saum	$5{,}88 \times 10^{-2}$	$3{,}29 \times 10^{-2}$	1,54	0,20	n.s.
Habitatheterogenität (Shannon-Index)	0,34	0,17	1,73	0,13	n.s.
(b) Gefährdete Arten ($R^2_{m/c}$ = 0,72–0,76)					
(Intercept)	0,22	0,48	0,42	.	n.s.
Pollenquellen	$3{,}18 \times 10^{-2}$	$8{,}19 \times 10^{-3}$	3,51	1,00	***
Abbruchkanten	$4{,}71 \times 10^{-3}$	$1{,}90 \times 10^{-3}$	2,23	0,77	*
(c) Oligolektische Arten ($R^2_{m/c}$ = 0,64–0,67)					
(Intercept)	0,77	0,41	1,68	.	n.s.
Pollenquellen	$2{,}68 \times 10^{-2}$	$7{,}16 \times 10^{-3}$	3,39	1,00	***
Abbruchkanten	$2{,}90 \times 10^{-3}$	$1{,}89 \times 10^{-3}$	1,38	0,34	n.s.

7 Diskussion

Unsere Studien zeigen die herausragende Bedeutung von Steinbrüchen für die Erhaltung der Artenvielfalt am Beispiel von Pflanzen, Amphibien, Tagfaltern und Wildbienen. Dies gilt nicht nur für die generelle Vielfalt an Arten, sondern insbesondere für die Vielfalt an spezialisierten und gefährdeten Arten. Auch die drei betreuten Abschlussarbeiten zu Libellen und Vögeln kommen zu ähnlichen Erkenntnissen (Kettermann 2017, Rasche 2019, Juffa 2021): Steinbruchgewässer wiesen eine höhere Artenvielfalt und höhere Abundanzen bei Libellen auf als dies für eine Zufallsauswahl von Gewässern in der umgebenden Landschaft der Fall war (Kettermann 2017). Besonders ausgeprägt waren diese Unterschiede bei Habitatspezialisten und Moorarten. Bei den Brutvögeln wiesen Steinbrüche eine genauso hohe Artenvielfalt wie – die für ihre artenreichen Brutvogelgemeinschaften bekannten (Brüggeshemke et al. 2022) – Kalkmagerrasen auf (Rasche 2019). Indikatorarten für die Steinbrüche waren unter anderem Hausrotschwanz (*Phoenicurus ochruros*) und Uhu (*Bubo bubo*) (Rasche 2019, Juffa 2021). Darüber hinaus kam die deutschlandweit vom Aussterben bedrohte Zippammer (*Emberiza cia*) im Untersuchungsgebiet nur in Steinbrüchen vor. Für Steinbrüche mit offenen Temporärgewässern war zudem der Flussregenpfeifer (*Charadrius dubius*) (siehe Titelseite) typisch (Juffa 2021).

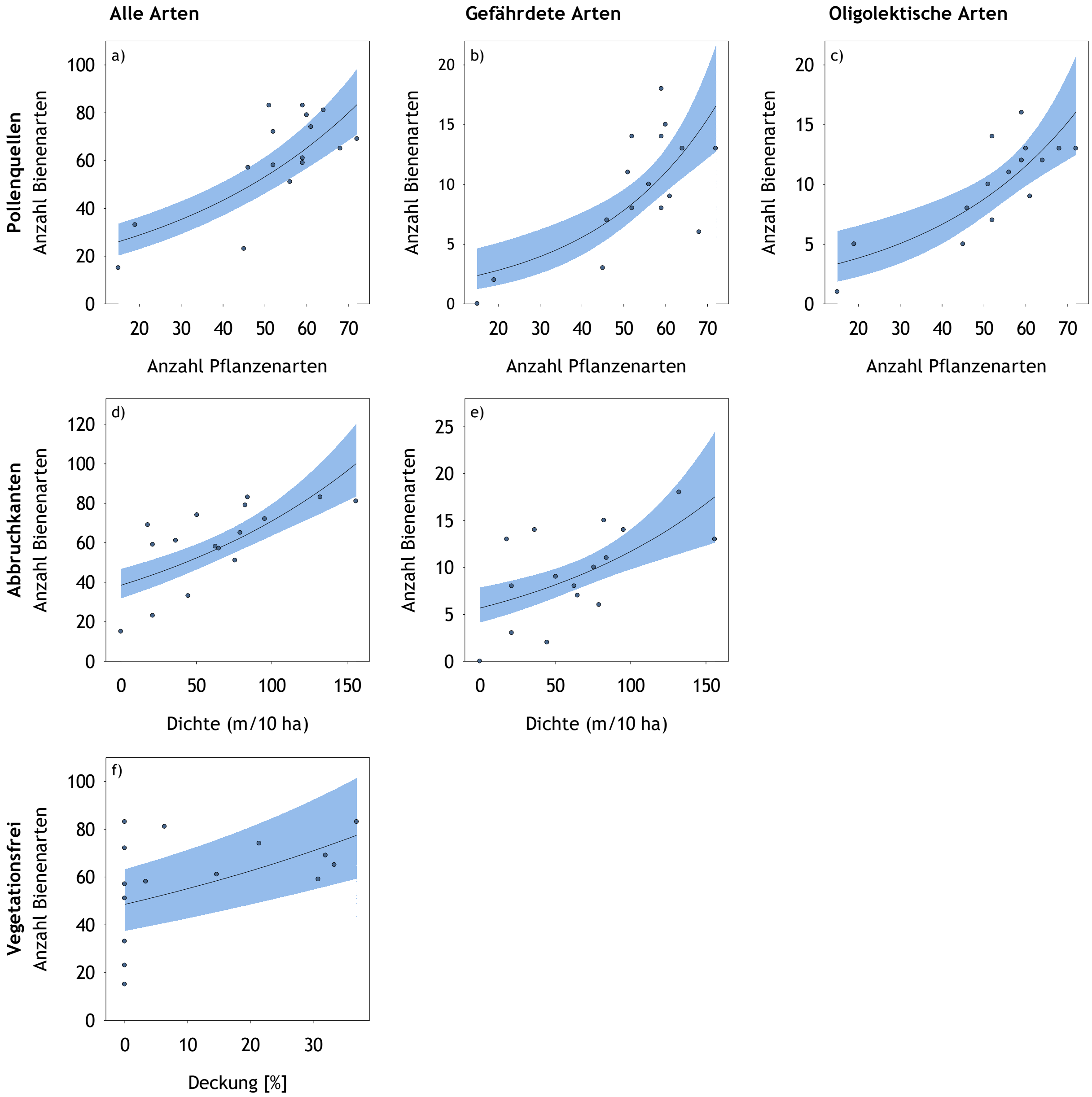

Abb. 12: Zusammenhang zwischen Anzahl aller, gefährdeter und oligolektischer Bienenarten und signifikanten Umweltparametern der multivariable Modelle ($N = 16$). Bezüglich der statistischen Kennwerte s. Tab. 13. R^2_m = durch feste Effekte erklärte Varianz, R^2_c = durch Zufallseffekte erklärte Varianz (Nakagawa et al. 2017). a) y = 0,02044 + 2,952362 × (Pollenquellen), $P < 0{,}001$, $R^2_m = 0{,}77$, $R^2_c = 0{,}87$; b) y = 0,03403 + 0,356758 × (Pollenquellen), $P < 0{,}001$, $R^2_m = 0{,}72$, $R^2_c = 0{,}82$; c) y = 0,02751 + 0,796513 × (Pollenquellen), $P < 0{,}001$, $R^2_m = 0{,}64$, $R^2_c = 0{,}64$; d) y = 0,24775 + 3,65082 × (Abbruchkanten), $P < 0{,}001$, $R^2_m = 0{,}74$, $R^2_c = 0{,}81$; e) y = 0,29296 + 1,73599 × (Abbruchkanten), $P < 0{,}001$, $R^2_m = 0{,}45$, $R^2_c = 0{,}45$; f) y = 0,01265 + 3,88289 × (vegetationsfrei), $P < 0{,}001$, $R^2_m = 0{,}41$, $R^2_c = 0{,}87$.Blaue Schraffur: 95-%-Konfidenzintervall.

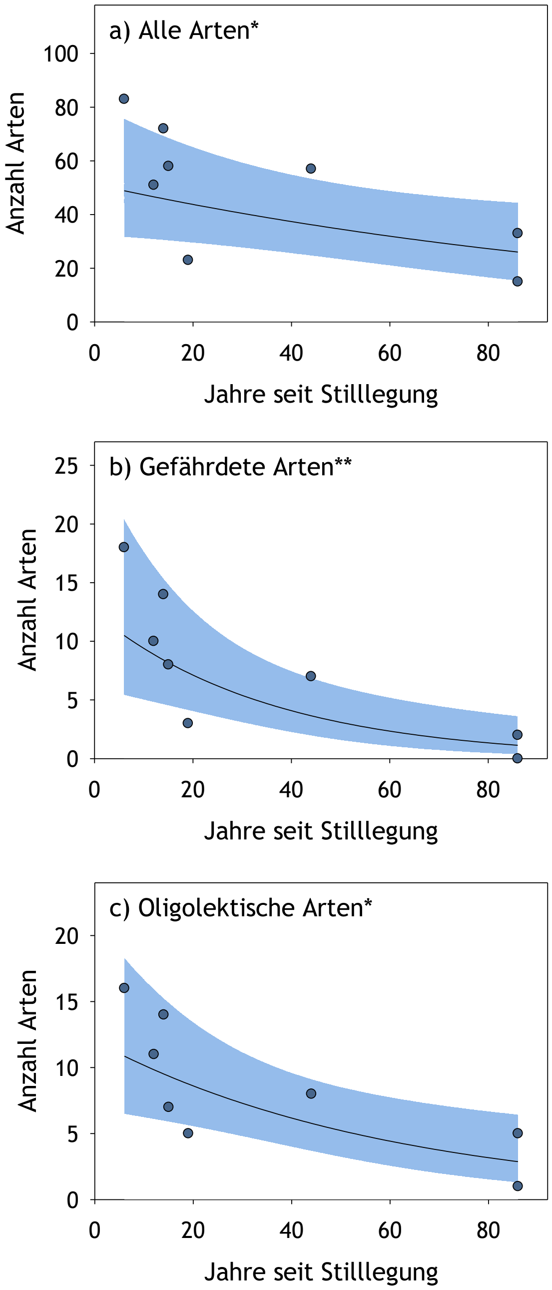

Abb. 13: Zusammenhang zwischen dem Umweltparamter 'Jahre seit Stillegung' und der Anzahl aller (a), gefährdeter (b) und oligolektischer Bienenarten (c) (N = 8). R^2_m = durch feste Effekte erklärte Varianz, R^2_c = durch Zufallseffekte erklärte Varianz (Nakagawa et al. 2017). a) y = 3,936564 – 0,007875 × (Jahre seit Stillegung), $P < 0,05$, $R^2_m = 0,31$, $R^2_c = 0,89$; b) y = 2,517935 – 0,027782 × (Jahre seit Stillegung), $P < 0,001$, $R^2_m = 0,74$, $R^2_c = 0,85$; c) y = 2,485633 – 0,016627 × (Jahre seit Stillegung), $P < 0,05$, $R^2_m = 0,61$, $R^2_c = 0,70$. Blaue Schraffur: 95-%-Konfidenzintervall.

Besonders wertvoll aus Naturschutzsicht sind die aktiven Steinbrüche, da sie reich an frühen Sukzessionsstadien mit einem warmen Mikroklima sind. Frühe Sukzessionsstadien sind in unserer stark eutrophierten Landschaft heutzutage ein Mangelfaktor und haben für viele konkurrenzschwache und wärmeliebende Arten eine elementare Bedeutung (Fartmann et al. 2021). Besonders eindrücklich konnte die Bedeutung aktiver Steinbrüche mit ihren frühen Sukzessionsstadien für den Argus-Bläuling (Kap. 5; Münsch & Fartmann 2022), die Blauflügelige Sandschrecke (*Sphingonotus caerulans*) (Kettermann & Fartmann 2018) und Wildbienen gezeigt werden (Kap. 6; Kettermann et al. 2022).

Basierend auf den eigenen Studien und den genannten Abschlussarbeiten sind folgende vier Habitate von zentraler Bedeutung für eine hohe Artenvielfalt und einen hohen Naturschutzwert von Steinbrüchen: 1. offene Felswände mit Nischen, 2. süd- und westexponierte Abbruchkanten/Erdwälle, 3. blumenreiche Ruderalvegetation und 4. Temporärgewässer mit ausgedehnten amphibischen Zonen. Die drei letzten genannten Habitate müssen gut besonnt sein und somit ein warmes Mikroklima aufweisen, damit sie ihre Bedeutung für den Biodiversitätsschutz voll entfalten können. Neben der Nährstoffarmut eines Habitats spielt genügend Licht eine zentrale Rolle für artenreiche Phytozönosen (Fartmann et al. 2021). Eine hohe Phytodiversität – insbesondere bei stark spezialisierten phytophagen Insekten wie Tagfaltern, Wildbienen oder Zikaden – und ein warmes Mikroklima fördern wiederum arten- und individuenreiche Insektengemeinschaften. Amphibien sind als poikilotherme Organismen ebenfalls auf ausreichend warme Lebensräume für die erfolgreiche Reproduktion angewiesen (Holtmann et al. 2017).

Offenen Felswänden kommt in Steinbrüchen vor allem als Brutplatz für einige Vogelarten, wie Dohle (*Corvus monedula*), Hausrotschwanz, Hohltaube (*Columba oenas*) oder Uhu, eine wichtige Bedeutung zu (Juffa 2021). Süd- und westexponierte Abbruchkanten/Erdwälle sind generell wichtige Nisthabitate für Insekten (Fartmann et al. 2021). Für Wildbienen sind sie sogar die wichtigsten Brutplätze: fast 60 % der heimischen Wildbienenarten nutzen offenen Boden als Reproduktionsort. Eine hohe Phytodiversität ist – wie bereits zuvor geschildert – ebenfalls ein zentraler Faktor für die Etablierung artenreicher Insektengemeinschaften. Der Wert der blumenreichen Ruderalvegetation für die Insektendiversität erklärt sich somit einerseits durch die Pflanzenartenvielfalt, andererseits durch einen gewissen Teil an Offenboden/Bodenskelett, der ein warmes Mikroklima begünstigt. Temporärgewässer mit ausgedehnten amphibischen Zonen weisen nicht nur das von Insekten und Amphibien gleichermaßen präferierte warme Mikroklima auf, sie sind auch frei von Fischen, da sie regelmäßig austrocknen. Fische zählen zu den Hauptprädatoren von Wasserinsekten wie Libellenlarven und den Fortpflanzungsstadien der Amphibien (Holtmann et al. 2017, 2018, 2019a). Die ausgedehnten amphibischen Zonen bieten darüber hinaus vielen konkurrenzschwachen Pflanzenarten gute Keimungsbedingungen (Holtmann et al. 2019b).

Im letzten Jahrhundert hat eine großflächige Homogenisierung vieler mitteleuropäischer Landschaften stattgefunden, was dramatische Verluste der Artenvielfalt nach sich zog (Poschlod 2017, Fartmann et al. 2021). Insbesondere in schon lange im Abbau befindlichen Steinbrüchen haben aber oft Arten der traditionell genutzten Kulturlandschaften überlebt, während sie in der Umgebung bereits ausgestorben sind (Beneš et al. 2003, Gilcher & Tränkle 2005, Novak & Konvička 2006, Münsch & Fartmann 2022). Argus-Bläuling (Kap. 5; Münsch & Fartmann 2022), aber auch Geburtshelferkröte oder Kreuzkröte (Kap. 4) sind klassische Beispiele für die Bedeutung von Steinbrüchen als Refugiallebensräumen in der heutigen Landschaft.

8 Handlungsempfehlungen zum biodiversitätsfördernden und nachhaltigen Management von Steinbrüchen

8.1 Alleinstellungsmerkmale von Steinbrüchen aus naturschutzfachlicher Sicht

Steinbrüche – insbesondere aktive mit langer Abbautradition – stellen oft Refugien für seltene Arten und Hotspots der Artenvielfalt in Mitteleuropa dar (Kap. 7). Sie sind durch extrem geringe Sukzessionsgeschwindigkeiten gekennzeichnet, da nach der Abbautätigkeit zunächst die Oberbodenauflage fehlt (Münsch & Fartmann 2022). Entsprechend bleiben frühe Sukzessionsstadien mit einem warmen Mikroklima mitunter über Jahrzehnte ohne weiteres Management erhalten. Eine so lange Persistenz früher Sukzessionsstadien ohne regelmäßige Nutzung ist im heutigen Mitteleuropa ein Alleinstellungsmerkmal. Aktive Steinbrüche weisen darüber hinaus eine zweite Besonderheit auf: sie sind durch eine hohe zeitliche und räumliche Dynamik gekennzeichnet. Eine derartige Dynamik ist inzwischen ebenfalls kaum noch zu finden, da dynamische Prozesse systematisch in der Landschaft unterbunden worden sind (Fartmann et al. 2021). Zu den verbliebenen Beispielen zählen die wenigen Auenabschnitte mit natürlicher Dynamik, unbefestigte Küstenabschnitte oder militärische Übungsplätze. Durch die Dynamik werden regelmäßig neue Pionierlebensräume geschaffen. Insbesondere viele unserer stark gefährdeten Arten sind auf diese Pionierhabitate mit ihren frühen Sukzessionsstadien angewiesen (Fartmann et al. 2021).

8.2 Management von Steinbrüchen

Aus Naturschutzsicht kommt der Erhaltung früher Sukzessionsstadien mit einem warmen Mikroklima in Steinbrüchen eine besondere Bedeutung zu. Von zentraler Bedeutung sind insbesondere vier Habitattypen: offene Felswände mit Nischen sowie jeweils besonnte Abbruchkanten/Erdwälle, blumenreiche Ruderalvegetation und Temporärgewässer mit ausgedehnten amphibischen Zonen (Kap. 7). In Steinbrüchen, in denen Temporärgewässer fehlen, sollten sie aktiv angelegt werden. Bei der Anlage der Gewässer ist darauf zu achten, dass sie ausreichend lange Wasser führen. Sie sollten nicht vor Juli austrocknen, um eine erfolgreiche Entwicklung der Amphibien zu gewährleisten. Aufgrund des Klimawandels werden Extremwetterereignisse wie Dürreperioden zunehmend häufiger (Fartmann et al. 2021), daher sollten auch einzelne Gewässer mit längerer Wasserführung angelegt werden. Auf Fischbesatz ist generell zu verzichten.

Sollten sich im Laufe der Zeit Gehölze etablieren, so ist eine mechanische Entbuschung durchzuführen (Münsch & Fartmann 2022). Der Gehölzschnitt kann im Steinbruch verbrannt werden, sofern eine anderweitige Nutzung – z.B. als Hackschnitzel für die Energieerzeugung (Helbing et al. 2015) – nicht möglich ist. Solche Brandstellen können sich für Arten wie den Argus-Bläuling zu wichtigen Fortpflanzungshabitaten entwickeln (Fartmann 2006, Münsch & Fartmann 2022). Die Anlage der Brandstellen ist allerdings oft genehmigungspflichtig. Eine andere Möglichkeit, ein zu starkes Gehölzaufkommen zu unterbinden, ist eine extensive Beweidung. Gerade in der Nähe von Siedlungen werden Steinbrüche regelmäßig für Freizeitaktivitäten, aber auch zur illegalen Entsorgung von Müll oder Gartenabfällen genutzt. Dies könnte durch eine Beweidung ebenfalls unterbunden werden. Überall dort, wo sich mächtigere Oberbodenauflagen entwickelt haben, sollten sie abgeschoben werden und in Form von Wällen angehäuft werden. Die aktive Einbringung von

Bodenmaterial und mögliche anschließende Bepflanzung/Aufforstung sind in den Steinbrüchen dagegen aus Gründen des Biodiversitätsschutzes grundsätzlich zu unterlassen.

Der Waschbär (*Procyon lotor*) ist in Mitteleuropa ein nicht-heimischer, omnivorer Prädator mit stark wachsenden Beständen (Klauer & Kriegs 2015, Salgado 2018). Das invasive Neozoon kann die Populationen von Kleinsäugern, Vögeln und Amphibien mitunter stark dezimieren (Salgado 2018, Fiderer et al. 2019). Auch in unseren Untersuchungen konnte ein neagtiver Einfluss auf die Amphibienpopulationen in Steinbrüchen festgestellt werden (eig. Beob.). In Regionen mit regelmäßigem Vorkommen des Waschbären schlagen wir eine intensive Bejagung vor. Zusätzlich können Metallkörbe, die während der Fortpflanzungsperiode der Amphibien über den Flachwasserbereichen der Gewässer installiert werden, Verluste minimieren. Neophyten spielten dagegen in unseren Studien in den Steinbrüchen kaum eine Rolle (eig. Beob.). Sofern kein Bodenmaterial in die Steinbrüche eingebracht wird, fassen Neophyten auf den flachgründigen Standorten nur schwer Fuß und Dominanzbestände treten kaum auf.

Insgesamt bieten Steinbrüche die einmalige Chance, mit geringem Aufwand eine Vielzahl spezialisierter Arten des nährstoffarmen Offenlandes langfristig zu erhalten. In Heiden, Kalkmagerrasen oder auf ehemaligen militärischen Übungsplätzen ist beispielsweise ein viel höherer finanzieller Aufwand notwendig, um ähliche Effekte zu erzielen, da die Sukzessionsgeschwindigkeiten aufgrund der tiefgründigeren Böden deutlich höher sind. In vielen Fällen ist das Management sogar nicht ausreichend, um das Aussterben der Arten zu verhindern. Ein Beispiel hierfür – unter vielen – ist der Argus-Bläuling (Münsch & Fartmann 2022).

8.3 Rechtliche Grundlagen des Gesteinsabbaus

Viele Herrichtungspläne für Gesteinsabbaustätten stammen noch aus einer Zeit als die herausragende Bedeutung von Steinbrüchen für den Biodiversitätsschutz erst in Ansätzen bekannt war (Poschlod et al. 1997). Entsprechend sehen viele dieser Pläne nach Beendigung des Abbaus eine Verfüllung und anschließende Aufforstung der Steinbrüche vor (Krauss et al. 2009, Tropek et al. 2010, Münsch & Fartmann 2022). Aufgrund der gegenwärtigen Biodiversitätskrise (IPBES 2019, Cardoso et al. 2020, Fartmann et al. 2021) sind derartige Vorgaben nicht mehr zeitgemäß. Entsprechend sollten auch bereits bestehende Herrichtungspläne gemäß den in Kap. 8.2 gemachten Vorgaben angepasst werden.

Die aktuelle Genehmigungspraxis zielt insbesondere auf die Erweiterung bestehender Steinbrüche oder die Neuanlage im Umfeld davon ab (Kettermann et al. 2022). Diese Praxis sollte beibehalten werden. Steinbrüche, die sich schon lange im Abbau befinden, stellen oft die letzten Refugien für Arten der traditionell genutzten Kulturlandschaften dar (Kap. 7). Durch die Erweiterung von Steinbrüchen oder die Entstehung von Steinbrüchen in der unmittelbaren Nachbarschaft können diese Arten leicht in die neu entstehenden Habitate einwandern und somit den langfristigen Fortbestand ihrer Populationen sichern.

Aktive Steinbrüche sind äußerst dynamische Lebensräume. Dies gilt es zwingend bei Genehmigungsverfahren zu beachten. Einerseits schafft der Gesteinsabbau immer wieder Lebensräume für viele hoch spezialisierte und gefährdete Arten, andererseits werden durch die Abbautätigkeit auch regelmäßig Lebensräume zerstört und Individuen getötet. Bis in die heutige Zeit werden allerdings Vorkommen von planungsrelevanten Arten in Bereichen, die für eine Erweiterung der Abbautätigkeit avisiert sind, von Steinbruchbetreibern und teilweise auch von Naturschutzbehörden als ein Hemmnis für eine Genehmigung eines solchen Abbaus angesehen (eig. Beob.). Dies führt teilweise immer noch dazu, dass Steinbruchbetreiber von vornherein versuchen, die Entstehung von Lebensräumen für planungsrelevante Arten im Keim zu ersticken. Dies gilt insbesondere für Gewässer.

Um dieses Dilemma aufzulösen und den Blick stärker auf den dynamischen Charakter von Steinbrüchen zu richten, haben verschiedene Institutionen des Naturschutzes (NABU, Landesbund für Vogelschutz) und der Rohstoffgewinnung im Jahr 2020 das gemeinsame Diskussionspapier „Natur auf Zeit in Rohstoffgewinnungsstätten“ veröffentlicht (https://www.nabu.de/news/2020/08/28465.html). Die Forderungen des Papiers sind aus Gründen des Biodiversitätsschutzes zu begrüßen und sollten zu einem Standard für Abbaustätten in Mitteleuropa werden. Im Prinzip geht es darum, die Bedeutung der Dynamik für die Erhaltung der Biodiversität in Steinbrüchen anzuerkennen und weniger eine einzelne Teilpopulation einer naturschutzrelevanten Art zu schützen, die durch den Abbau möglicherweise negativ betroffen ist. Vielmehr soll das langfristige Überleben der Gesamtpopulation der Art in einem Steinbruch oder einem Steinbruchverbund im Mittelpunkt stehen.

Zusammenfassung

In Deutschland fehlen generell zukunftsfähige Konzepte zur Erhaltung der Artenvielfalt, die sowohl die Auswirkungen des Landnutzungs- als auch des Klimawandels hinreichend berücksichtigen. Dies gilt auch für Steinbrüche, die aufgrund des globalen Baubooms und damit zusammenhängend einer stark gestiegenen Nachfrage nach Baumaterial – wie Zement oder Steinen – eine zunehmend größere Bedeutung erlangen.

Am Beispiel von Pflanzen, Amphibien, Tagfaltern und Wildbienen wurde in diesem Projekt untersucht, welche Faktoren der Habitat- und Landschaftsqualität für die Ausbildung artenreicher Biozönosen in Steinbrüchen verantwortlich sind. Ein besonderer Fokus lag hierbei auf der Betrachtung gefährdeter Arten. Aufbauend auf den eigenen Studien und Erkenntnissen aus Abschlussarbeiten zu Vögeln und Libellen wurden wissenschaftlich-fundierte Handlungsempfehlungen zum biodiversitätsfördernden und nachhaltigen Management von Steinbrüchen in Mitteleuropa erarbeitet.

Unsere Studien zeigen, das Steinbrüche – insbesondere aktive mit langer Abbautradition – oft Refugien für seltene Arten und Hotspots der Artenvielfalt in Mitteleuropa sind. Sie sind durch eine extrem geringe Sukzessionsgeschwindigkeiten gekennzeichnet, da nach der Abbautätigkeit zunächst eine Oberbodenauflage fehlt. Entsprechend bleiben frühe Sukzessionsstadien mit einem warmen Mikroklima mitunter über Jahrzehnte ohne weiteres Management erhalten. Eine so lange Persistenz früher Sukzessionsstadien ohne regelmäßige Nutzung ist im heutigen Mitteleuropa ein Alleinstellungsmerkmal. Aktive Steinbrüche weisen darüber hinaus eine zweite Besonderheit auf: sie sind durch eine hohe zeitliche und räumliche Dynamik gekennzeichnet.

Aus Naturschutzsicht hat die Erhaltung früher Sukzessionsstadien mit einem warmen Mikroklima in Steinbrüchen eine besondere Relevanz. Von zentraler Bedeutung sind insbesondere vier

Habitattypen: offene Felswände mit Nischen sowie jeweils besonnte Abbruchkanten/Erdwälle, blumenreiche Ruderalvegetation und Temporärgewässer mit ausgedehnten amphibischen Zonen. Insgesamt bieten Steinbrüche die einmalige Chance, mit geringem Aufwand eine Vielzahl spezialisierter Arten des nährstoffarmen Offenlandes langfristig zu erhalten.

Viele Herrichtungspläne für Gesteinsabbaustätten stammen noch aus einer Zeit als die herausragende Bedeutung von Steinbrüchen für den Biodiversitätsschutz erst in Ansätzen bekannt war. Entsprechend sehen viele dieser Pläne nach Beendigung des Abbaus eine Verfüllung und anschließende Aufforstung der Steinbrüche vor. Aufgrund der gegenwärtigen Biodiversitätskrise sind derartige Vorgaben nicht mehr zeitgemäß. Entsprechend sollten auch bereits bestehende Herrichtungspläne gemäß den zuvor gemachten Vorgaben angepasst werden.

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Anhang I: Publikationen

Münsch & Fartmann (2022): *Insect Conservation and Diversity* 15: 200–212.

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Limestone quarries are the most important refuge for a formerly widespread grassland butterfly

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Abstract. 1. Calcareous grasslands have an outstanding value for nature conservation. However, during the last century, they have suffered from severe area loss, fragmentation and degradation.

2. Here, we studied the influence of macroclimate, landscape quality and habitat quality on populations of the Silver-studded Blue, *Plebejus argus*, in calcareous grasslands and limestone quarries in a Central European landscape.

3. Our study revealed that limestone quarries, especially those being actively managed, are the most important refuge for *P. argus*. Originally, the species was common in calcareous grasslands across the study area. More recently, however, patch occupancy was five times higher at quarries compared to calcareous grasslands and mean adult abundance nearly four times higher at occupied quarries than at occupied grasslands. The key driver of patch occupancy and adult abundance was a high abundance of the host plant. Adult abundance, additionally, increased with a sparse vegetation and a high cover of bedrock.

4. The deterioration of habitat quality due to abandonment and decreasing grazing intensity has resulted in a strong decline of *P. argus* in calcareous grasslands. In contrast, quarries exhibit a very low successional speed due to their shallow soils. Hence, they are characterised by a high habitat quality for *P. argus*, i.e. dense stands of the host plant *L. corniculatus*, which grow on skeletal soils providing warm microclimatic conditions.

5. Preserving limestone quarries with their early-successional stages is of crucial importance for the conservation of *P. argus*.

Key words. Calcareous grassland, early-successional stage, habitat quality, host-plant abundance, microclimate, patch connectivity.

Introduction

Calcareous grasslands are among the most species-rich habitat types across Europe (Poschlod & Wallis de Vries, 2002; Wallis de Vries *et al*., 2002). However, during the last century, agricultural intensification, eutrophication, afforestation and abandonment of traditional land use have caused a severe loss, fragmentation and degradation of calcareous grasslands (Poschlod & Wallis de Vries, 2002; Wallis de Vries *et al*., 2002; Veen *et al*., 2009). Due to their status as biodiversity hotspots and the threats they face, they are protected by the EU Habitats Directive (European Commission, 1992). They are of prime importance for plants and many groups of insects (Wilson *et al*., 2012; Bonari *et al*., 2017; Löffler *et al*., 2020; Poniatowski *et al*., 2020; Helbing *et al*., 2021). For example, about 50% of all native European butterfly species occur in calcareous grasslands (van Swaay, 2002; van Swaay *et al*., 2006).

Butterflies are characterised by very specific habitat requirements (García-Barros & Fartmann, 2009; Dennis, 2010). Host-plant availability and microclimatic conditions are the most important predictors of butterfly habitat quality (García-Barros & Fartmann, 2009; Curtis *et al*., 2015). The microclimate within a butterfly habitat is mainly influenced by vegetation structure (García-Barros & Fartmann, 2009; Scherer *et al*., 2021), which usually depends on land use (Dover & Settele, 2009). Most thermophilous habitat-specialist butterflies require warm microhabitats for oviposition

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(e.g. Roy & Thomas, 2003; Krämer *et al*., 2012a). This is especially true for regions with a cool macroclimate, such as most of western or Central Europe. Here, they often depend on the earliest successional stages (Thomas, 1993; Roy & Thomas, 2003) and are among the most strongly declining species (Eskildsen *et al*., 2015; Habel *et al*., 2019). Besides habitat quality, the distribution of habitat-specialist butterflies in cultivated landscapes usually depends on patch size and patch connectivity (Eichel & Fartmann, 2008; Stuhldreher & Fartmann, 2014; Poniatowski *et al*., 2018b).

The Silver-studded Blue, *Plebejus argus* (Linnaeus 1758), is a thermophilous habitat specialist, and calcareous grasslands are one of its main habitats (Asher *et al*., 2001; Nunner, 2013). In western and Central Europe, the species has disappeared from many areas in recent decades (Bos *et al*., 2006; Fox *et al*., 2006; Meineke, 2020). Habitat loss and the deterioration of habitat quality due to the abandonment of traditional land use are assumed to be the main drivers of the decline (Asher *et al*., 2001; Stefanescu *et al*., 2009). For Great Britain, detailed studies on the habitat requirements of *P. argus* in calcareous grasslands are available (Thomas 1985a, 1985b; Lewis *et al*., 1997; Dennis & Sparks, 2006). Based on this research, the species depends on early-successional habitats, which provide warm microclimatic conditions for larval development.

In this article, we studied patch occupancy and abundance of *P. argus* in calcareous grasslands and limestone quarries in a Central European landscape with intensive agriculture and forestry. We analysed the influence of macroclimate, landscape quality and habitat quality on patch occupancy and abundance of the species. The aim of our study was to compare the environmental conditions of occupied and vacant habitat patches to determine the drivers of local population extinctions. Based on our results, we make management recommendations for the conservation of *P. argus* in Central European landscapes.

Materials and methods

Study area

The study area, the Diemel Valley and directly adjoining Brilon Plateau, is about 510 km^2 large and located in Central Germany along the border between the federal states of North Rhine-Westphalia and Hesse (51°22’N/8°28’E and 51°38’N/9°28’E) (Fig. 1). It exhibits the largest area of semi-dry calcareous grasslands (∼775 ha) in the northern half of Germany (Fartmann, 2004, 2006). Open limestone quarries are also widespread (∼205 ha). Both calcareous grasslands and limestone quarries are surrounded by a matrix of intensively used agricultural land and forests (Fartmann, 2004; Poniatowski *et al*., 2020).

The climate is subatlantic and varies greatly with elevation (Fartmann, 2004). The Brilon Plateau (360–600 m a.s.l.) is the coolest (annual mean temperature: 7.9 °C) and wettest (annual precipitation: 1073 mm) part of the study area [meteorological values are long-term means (1981–2010) and were derived from 1-km^2 grid datasets; Germany’s National Meteorological Service, pers. comm.]. The Upper Diemel Valley (200–600 m a.s.l.) is similarly cool (8.1 °C), but the precipitation is lower

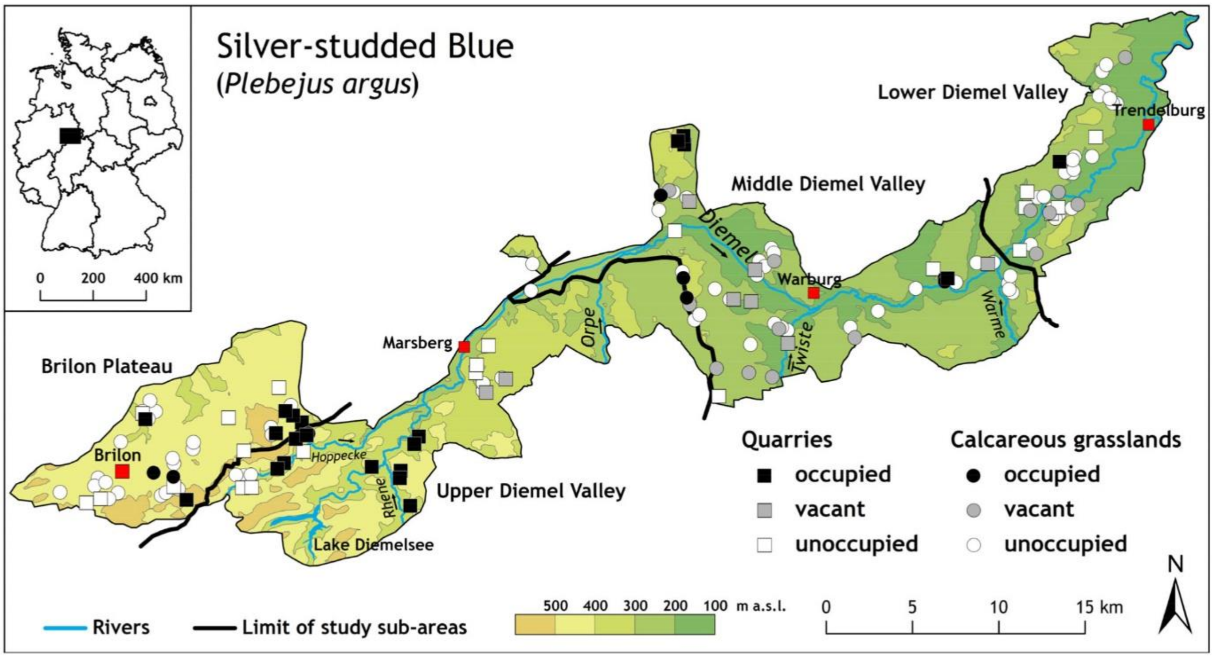

Fig 1. Location of the study area in Germany (inlay) and distribution of quarries ($n = 51$) and calcareous grasslands ($n = 99$) in the study area. Towns are indicated by red squares.

(845 mm). In the Middle Diemel Valley (140–400 m a.s.l.), the precipitation is even lower (737 mm) and the temperature is higher (8.8 °C). The Lower Diemel Valley (100–375 m a.s.l.) is the warmest (9.0 °C) part of the study area. Here, precipitation (788 mm) is slightly higher compared to the Middle Diemel Valley (Stuhldreher & Fartmann, 2018).

Calcareous grasslands are widespread in all four subareas (Glöckner & Fartmann, 2003; Fartmann, 2004, 2006). However, almost two-thirds (61%) of the limestone quarries are situated in the coolest subareas, the Brilon Plateau and the Upper Diemel Valley. Additionally, except three, all quarries still used for active mining are located in these subareas. Further information on the Brilon Plateau is available in the study by Glöckner and Fartmann (2003). A detailed description of the Diemel Valley is given by Fartmann (2004, 2006).

Study species

The Silver-studded Blue, *Plebejus argus* (Linnaeus 1758), is a lycaenid butterfly with a Palearctic distribution ranging from England eastwards across temperate Asia and Siberia to Japan, and from the Mediterranean region (36° N) to Fenno-Scandinavia (69° N) (Nunner, 2013; Meineke, 2020). In our study area, the species is univoltine and has a flight peak between mid-June and mid-July (Fartmann, 2004).

Plebejus argus colonises nutrient-poor, open habitats, such as degraded raised bogs, heathlands and calcareous grasslands (Nunner, 2013; Schirmel & Fartmann, 2014). Within its habitats, the species is dependent on early-successional stages with low-growing, sparse vegetation and a high proportion of bare ground or bedrock for oviposition (Thomas, 1985a, 1985b; Asher *et al*., 2001; Schirmel & Fartmann, 2014). Females deposit their eggs singly close to their host plants (Thomas, 1985b; Asher *et al*., 2001). On calcareous soils, *Lotus corniculatus* is the main host plant (Thomas, 1985a; Thomas *et al*., 1999; Asher *et al*., 2001). Within our study area, the occurrence of *P. argus* is restricted to calcareous grasslands and limestone quarries with *L. corniculatus* as the most important host plant (Fartmann, 2004). *Plebejus argus* hibernates in the egg stage, and larvae hatch towards the end of March (Bos *et al*., 2006). Both the caterpillars and pupae have a strong mutualistic relationship with ants of the genus *Lasius* (Hymenoptera: Formicidae). On calcareous soils, *Lasius alienus* is usually the main host (Jordano *et al*., 1992; Jordano & Thomas, 1992). From the end of May to early June, the larvae pupate near or most often within the ant nests (Asher *et al*., 2001). Adults hatch after 13–20 days of pupation (Bos *et al*., 2006).

In the first half of the 20th century, *P. argus* was common and widespread in calcareous grasslands of the Diemel Valley (Retzlaff, 1973). However, already by the end of the last century, the species had become very rare in calcareous grasslands in this part of the study area (Fartmann, 2004). In contrast, in limestone quarries, *P. argus* still occurred regularly in high densities. For the Brilon Plateau, no data on the distribution of *P. argus* during the last century are available (Glöckner & Fartmann, 2003). In Hesse and North Rhine-Westphalia, the species is considered vulnerable and endangered, respectively (Lange & Brockmann, 2009; Schumacher, 2011).

Sampling design

In this study, we surveyed a total of 150 patches: 99 calcareous grasslands (GRASS) and 51 limestone quarries (QUARRY). Data on the occurrence of GRASS and QUARRY in the study area were derived from Glöckner and Fartmann (2003), Fartmann (2004) and Stuhldreher and Fartmann (2018). Data on historic records of *P. argus* were taken from Retzlaff (1973), Glöckner and Fartmann (2003) and Fartmann (2004). The data were used to identify all formerly occupied patches in the study area. Patches were regarded as discrete if they were separated from each other by more than 50 m of non-habitat, such as forest, improved grassland and arable fields (e.g. Krämer *et al*., 2012b; Poniatowski *et al*., 2018b). Additionally, we distinguished the habitat patches based on their occupancy by *P. argus* (cf. 'Patch occupancy' section) into the six following habitat types: (i) occupied QUARRY, (ii) occupied GRASS, (iii) vacant QUARRY, (iv) vacant GRASS, (v) unoccupied QUARRY and (vi) unoccupied GRASS (Fig. 1). Vacant patches were occupied by *P. argus* in the past whereas the former status of the unoccupied patches is unknown. In order to determine the drivers of local population extinction only occupied and vacant patches were used for the analysis of the species' habitat characteristics. Further details on the sampling of *P. argus* and its patch occupancy are given in the 'Butterfly sampling' section.

Environmental conditions

Macroclimate. Characteristics of the local climate of each patch (mean number of frost days, mean annual precipitation and mean annual temperature) were derived from 1-km^2 grid datasets of Germany's National Meteorological Service (pers. comm.), which contain 10-year (2010–2019) mean values. The mean elevation (m a.s.l.) of the patches was calculated from topographic maps using ArcGIS 10.2.

Landscape and habitat quality. For each occupied and vacant patch, we assessed several parameters of landscape and habitat quality (Tables 1 and 2). Landscape quality parameters were ascertained for unoccupied patches as well (Supporting Information Table S1 and Table S2). Concerning land-use of GRASS and QUARRY, we distinguished between managed and abandoned patches. The former comprised grasslands regularly grazed by sheep and goats (at least once per year) and quarries still used for mining (Table 1; Supporting Information Table S1). In managed quarries, partly shrub removal was also regularly carried out to avoid excessive shrub encroachment.

The landscape-quality parameters patch size and patch connectivity were determined on the basis of aerial photographs using ArcGIS 10.2 (Table 2; Supporting Information Table S2). The size of the patches varied between 0.2 and 15.8 ha (mean: 2.6 ± 0.3 ha). Connectivity of the patches was measured as the geometric mean of the next three populated patches (Eichel & Fartmann, 2008; Scherer *et al*., 2021). Edge-to-edge distances from the focal patch to the three other patches were computed using the proximity-analysis tool 'near table' in ArcGIS 10.2.

Table 1. Absolute and relative frequencies of the nominal variables 'habitat type' and 'land use' at occupied and vacant patches of *Plebejus argus*.

	Occupied ($n = 29$)		Vacant ($n = 22$)		
Parameter	*N*	%	*N*	%	*P*
Habitat type					*
QUARRY	21	72.4	8	27.6	
GRASS	8	36.4	14	63.6	
Land use					
QUARRY					*
Managed	9	100.0	0	0.0	
Abandoned	12	60.0	8	40.0	
GRASS					*
Managed	8	57.1	6	42.9	
Abandoned	0	0.0	8	100.0	

Differences in absolute frequencies between habitat types were analysed with Fisher's exact test. Significance levels are indicated as follows: $*P < 0.05$.

Connectivity of the patches varied between 0.3 and 12.7 km (mean: 4.2 ± 0.2 km).

We sampled habitat-quality parameters once at the beginning of July 2019 (Table 2). On each occupied and vacant patch, we recorded several vegetation-structure parameters, abundance of the main host plant (*L. corniculatus*) and soil depth at three randomly selected plots of 4 m^2 (2 m × 2 m). The following parameters of horizontal vegetation structure were estimated (in 5% steps): the cover of herbs, grasses, litter, mosses, small shrubs (<0.5 m) and bare ground as well as gravel, stones and rocks (hereinafter termed 'bedrock'). In cases where cover was above 95% or below 5%, 2.5% steps were used. The mean value of the average vegetation height was calculated from measurements at three random points within each plot. Vegetation density was estimated using a wire-framed box (50 cm × 30 cm × 30 cm), which was open on all sides except the back. Horizontal wires on the front side of the box divided it into six height layers of 5 cm each to estimate the vegetation density between 0 and 30 cm above ground. The cover of each layer was viewed horizontally against the bright back of the box, using the same classes as for the horizontal vegetation structure (Fartmann *et al*., 2012; Löffler & Fartmann, 2017). Soil depth was measured at the centre of each plot using a metal rod with length marks (Poniatowski *et al*., 2020). For further analyses, we calculated mean values of the three plots.

We sampled sunshine duration and air temperature as microclimatic parameters. The potential daily sunshine duration for the month June was measured in the field with an accuracy of ¼ h using a horizontoscope (Streitberger & Fartmann, 2015). Air temperature was ascertained for each of the four habitat types. The patches were randomly selected and the number of replicates per habitat type was five. We installed Hygrochron temperature data loggers (iButton, Maxim/Dallas, DS1923, USA) 10 cm above ground. They were placed in a self-constructed radiation shield to protect the sensor from direct sunlight and precipitation (Stuhldreher & Fartmann, 2018). The radiation shield consisted of a white metal case with an integrated Styrofoam insulation (1 cm thick) to prevent the data loggers from overheating on sunny days. The data loggers recorded air temperature once every hour with an accuracy of 0.5 °C for 14 days from 23 July until 5 August 2019.

Since the data loggers were placed in distinct patches, we treated them as statistically independent units. The values recorded by one and the same data logger, however, were not independent of each other. Hence, we averaged the hourly recorded values of each logger over the entire measurement period and used these averages for our analyses. Accordingly, differences between the mean values of distinct data loggers reflect the microclimatic differences between patches (Stuhldreher & Fartmann, 2018). Furthermore, we analysed microclimatic differences between habitat types for daytime and night-time separately. As the thermal effects of solar radiation are weak shortly after sunrise, but especially in summer the aftereffects last a relatively long time until sunset, daytime was defined as the period from two hours after sunrise to sunset (8:00 a.m. to 9:00 p.m.). Consequently, all recorded values within this period were assigned to daytime, while all other measurements (10:00 p.m. to 7:00 a.m.) were assigned to night-time.

Butterfly sampling

Patch occupancy. In 2018 and 2019, respectively, all patches of GRASS ($n = 99$) and QUARRY ($n = 51$) in the study area were surveyed up to two times during the peak of the species' flight period between mid-June and the beginning of July, with a time interval of at least two weeks between each survey (cf. Öckinger, 2006; Eichel & Fartmann, 2008). To assess the occupancy of *P. argus*, transect walks were done between 10 a.m. and 5 p.m. under suitable weather conditions (dry, sunny days with temperatures >18 °C and low wind speed). In every patch, adults of *P. argus* were recorded walking in loops covering all open habitat structures with a width of 5 m between each loop. Only GRASS and QUARRY without evidence for occupancy of the species during the first survey were investigated a second time. According to Poniatowski *et al*. (2018b), a patch was classified as occupied if at least three adults (as an indicator for an indigenous population) were detected.

Abundance. Based on the patch occupancy survey, we sampled the abundance of adult *P. argus* in all occupied patches in 2019. Butterflies were sampled in plots of 500 m^2 (20 m × 25 m) size at that part of the patch with the highest adult density using standardised transect counts (Pollard & Yates, 1993; Krämer *et al*., 2012b). We recorded the number of adult individuals inside the plots in loops with a width of 5 m. Each transect count took 15 min, excluding identification time for critical individuals (Krämer *et al*., 2012b). All plots were visited twice throughout the peak of the species' flight period (mid-June to early July) between 10:00 a.m. and 5:00 p.m. and only during suitable weather conditions (cf. 'Patch occupancy' section). The chronological order of the sampling of the transect plots was based on the climatic gradient across the four subareas (Lower Diemel Valley > Middle Diemel Valley > Upper Diemel

Table 2. Mean values (±SE) of all numerical environmental parameters at the four habitat types. Differences among habitat types were analysed by LMM/GLMM and subsequent Tukey contrasts, see materials and methods for details.

	Occupied ($n = 29$)		Vacant ($n = 22$)				
Parameters	QUARRY ($n = 21$)	GRASS ($n = 8$)	QUARRY ($n = 8$)	GRASS ($n = 14$)	P	r_S	Used variables
Macroclimate							
Elevation (m a.s.l.)	380.8 ± 17.7^{a}	314.1 ± 39.8^{ab}	252.9 ± 21.0^{b}	221.5 ± 10.4^{b}	***	−0.82	
Frost days[a]	80.2 ± 1.4^{a}	77.4 ± 1.9^{ab}	74.4 ± 1.6^{b}	72.7 ± 0.8^{b}	***	−0.86	► Temperature
Precipitation (mm)[b]	746.8 ± 20.4^{a}	730.4 ± 34.3^{ab}	653.3 ± 11.8^{b}	658.0 ± 7.6^{b}	**	−0.83	
Temperature (°C)[c]	9.1 ± 0.1^{a}	9.3 ± 0.2^{ab}	9.6 ± 0.1^{b}	9.7 ± 0.1^{b}	***	1.00	
Landscape quality							
Patch size (ha)	1.0 ± 0.1	0.8 ± 0.2	1.4 ± 0.2	2.7 ± 0.7	n.s.		
Patch connectivity (km)[d]	1.8 ± 0.4^{a}	3.0 ± 0.5^{ab}	4.8 ± 0.6^{b}	6.1 ± 0.7^{b}	***		
Habitat quality							
Sunshine (h)[e]	13.4 ± 0.5^{a}	12.3 ± 0.7^{a}	10.4 ± 0.8^{b}	11.8 ± 0.5^{a}	**		
Vegetation structure							
Vegetation density (%)							
0–5 cm	65.3 ± 2.7^{a}	71.0 ± 3.4^{ab}	86.7 ± 5.3^{bc}	94.6 ± 2.1^{c}	***	0.79	
10–15 cm	27.9 ± 2.7^{a}	19.0 ± 2.1^{a}	49.2 ± 8.8^{b}	52.9 ± 6.6^{b}	***	1.00	► Vegetation density, 10–15 cm
20–25 cm	5.0 ± 0.9^{ab}	2.3 ± 0.6^{a}	14.3 ± 5.7^{ab}	17.1 ± 5.5^{b}	*	0.84	
Vegetation height (cm)	14.3 ± 1.0^{a}	11.5 ± 1.2^{a}	17.3 ± 2.1^{ab}	19.8 ± 2.3^{b}	*	0.81	
Cover (%)							
Bare ground	11.0 ± 1.8^{ab}	21.7 ± 3.2^{a}	6.3 ± 1.2^{b}	4.9 ± 0.8^{b}	***		
Bedrock[f]	20.3 ± 2.4^{a}	5.7 ± 1.6^{b}	5.0 ± 1.6^{b}	2.1 ± 0.8^{b}	***		
Small shrubs (<0.5 m)	0.8 ± 0.3^{a}	0.9 ± 0.3^{ab}	2.8 ± 1.1^{ab}	3.7 ± 0.9^{b}	**		
Herbs	51.7 ± 1.8^{a}	41.1 ± 2.9^{b}	49.3 ± 1.9^{ab}	41.6 ± 1.8^{b}	***		
Grasses	15.1 ± 1.9^{a}	30.0 ± 4.9^{b}	37.1 ± 3.7^{b}	51.2 ± 2.8^{c}	***	−0.83	
Host plant *L. corniculatus*	38.1 ± 2.6^{a}	24.2 ± 3.7^{b}	15.7 ± 3.3^{bc}	8.9 ± 1.2^{c}	***	1.00	
Mosses	26.1 ± 3.4^{ab}	17.3 ± 4.1^{a}	36.5 ± 6.3^{b}	38.6 ± 5.3^{b}	*	−0.70	► *Lotus corniculatus*
Litter	4.5 ± 1.4^{a}	5.4 ± 2.7^{a}	30.4 ± 7.9^{b}	33.0 ± 6.0^{b}	***	−0.74	
Soil depth (cm)	5.3 ± 0.6^{a}	7.2 ± 0.9^{a}	10.4 ± 1.6^{ab}	18.7 ± 1.6^{b}	***	−0.73	

Habitat types without consistent letters indicate significant differences ($P < 0.05$). Significant differences between the habitat types are also indicated by bold type. Significance levels are indicated as follows: n.s. not significant, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

[a] Mean no. of frost days/a.

[b] Mean annual precipitation (mm).

[c] Mean annual temperature (°C).

[d] Mean distance to the next three occupied patches.

[e] Mean potential duration of daily sunshine in June.

[f] Gravel, stones and rocks.

Valley > Brilon Plateau) in order to take phenological differences into account. For statistical analyses, the maximum abundance of the two counts was used (Streitberger *et al*., 2012; Weking *et al*., 2013).

Statistical analysis

Differences in absolute frequencies between the nominal variables ‘habitat type’ and ‘land use’ of occupied, vacant and unoccupied patches were analysed with Fisher's exact test (Table 1; Supporting Information Table S1). For detecting significant differences in environmental parameters (Table 2; Table S2; Fig. 2) and butterfly abundance between the habitat types, (generalised) linear mixed-effect models (GLMM; LMM) were applied (R packages lme4, Bates *et al*., 2020) with ‘subarea’ as a random factor. Habitat type served as a nominal fixed factor, and the analysed parameters were used as dependent variables. Depending on the distribution of the variables, binomial (percentage data), Poisson (count data) or Gaussian (for square-root- or log-transformed variables with normal distribution) models were applied with the respective standard link functions. For reducing overdispersion within the models (binomial/Poisson), observation-level random effects were added as a random factor (Harrison, 2014, 2015). The overall effect of the dependent variables on habitat type was analysed by comparing the full models with reduced models without ‘habitat type’ as the fixed factor and applying likelihood-ratio tests. Pairwise differences between the habitat types were detected by applying Tukey contrasts (glht function, R package multcomp, Hothorn *et al*., 2020).

To determine which environmental parameters explained patch occupancy and abundance of *P. argus*, we fitted GLMM (binomial and negative-binomial, respectively). To avoid model overfitting, in both cases, we performed three different models, each containing a different set of environmental parameters (macroclimate, landscape quality and habitat quality, Table 2; Stuhldreher & Fartmann, 2014). Finally, all significant variables

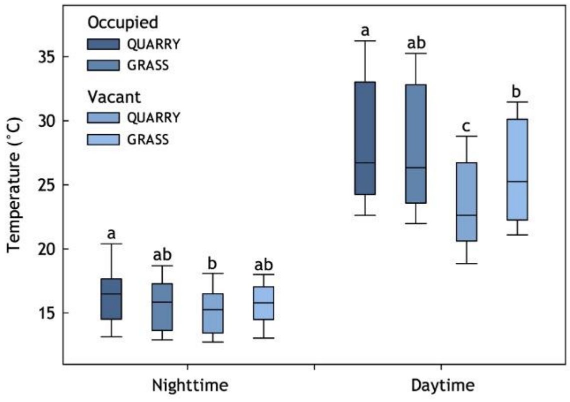

Fig 2. Differences in hourly mean air temperature during night-time (10 p.m. to 7 a.m.) and daytime (8 a.m. to 9 p.m.) between the four habitat types (measurement period: 23 July to 5 August 2019). The boxes show the median and the first and third quartile, the whiskers indicate the 10th and 90th percentile. Differences among habitat types were analysed by GLMM and subsequent Tukey contrasts, see 'Statistical analysis' section for details. Habitat types without consistent letters indicate significant differences ($P < 0.05$).

of the macroclimate, landscape-quality and habitat-quality models were incorporated into a synthesis model. For all GLMM, the variables 'habitat type' and 'subarea' were used as random factors (Crawley, 2007). In order to increase model robustness and identify the most important environmental parameters, we conducted model averaging based on an information-theoretic approach (Burnham & Anderson, 2002; Grueber *et al*., 2011). Model averaging was conducted using the dredge function (R package MuMIn, Bartón, 2020) and included only top-ranked models within $\Delta AIC_C < 3$ (Grueber *et al*., 2011). Prior to multivariable analyses, we implemented Spearman's rank correlations (r_S) between all numerical environmental parameters to identify possible intercorrelations. If parameters were strongly intercorrelated ($|r_S| > 0.7$), only the most important variable was used in GLMM analyses (Table 2). All statistical analyses were performed using R 3.5.2 (R Development Core Team, 2019).

Results

Patch occupancy

5wIn total, 29 (19%) of the 150 studied patches were occupied by *P. argus* and 22 (15%) were vacant. All other 99 patches (66% of all surveyed patches) were unoccupied by *P. argus*, but the former occupation status is unknown. Patch occupancy was five times higher at QUARRY ($n = 21$, 41% of all surveyed quarries) compared to GRASS ($n = 8$, 8% of all surveyed grasslands) (Table 1; Supporting Information Table S1). The frequency of occupied and vacant patches differed between QUARRY and GRASS; at QUARRY, the number of occupied patches was higher and those of vacant patches were lower. Additionally, active management favoured the occurrence of the species. Patch occupancy was higher at managed QUARRY than at abandoned QUARRY. At GRASS, even all occupied patches were managed ones (Table 1). The frequency of unoccupied patches also differed between QUARRY and GRASS, as the majority of unoccupied patches were GRASS patches (Table S1).

Except patch size, all metric environmental parameters differed among the four habitat types (Table 2; Fig. 2). Especially, occupied patches varied strongly from vacant ones; additionally, occupied QUARRY was characterised by the most extreme environmental conditions. All macroclimatic parameters were intercorrelated (Table 2). Occupied QUARRY was situated at the highest elevations and was characterised by the highest number of frost days and annual precipitation as well as the lowest temperature. Occupied QUARRY differed from vacant patches. Occupied GRASS had an intermediate position. Occupied QUARRY had the highest connectivity, differing from vacant patches. In contrast, occupied GRASS did not differ in any of the macroclimatic and landscape-quality parameters from any of the three other habitat types.

When comparing the landscape-quality parameters of all six habitat types, unoccupied patches differed from occupied patches. Unoccupied QUARRY patches were larger than occupied patches. Both unoccupied QUARRY and unoccupied GRASS were less connected than occupied QUARRY and showed similar patch connectivity values as vacant patches. Unoccupied QUARRY was situated at higher elevations than vacant patches. Unoccupied GRASS did not differ in macroclimatic parameters from any of the five other habitat types (Supporting Information Table S2).

Habitat-quality parameters were also strongly intercorrelated (Table 2). Usually, they reflected a gradient from occupied QUARRY to occupied GRASS to vacant patches. Along this gradient, vegetation density, vegetation height, the cover of small shrubs, mosses, grasses and litter as well as soil depth increased. In contrast, the cover of bare ground, bedrock, herbs and the host plant *L. corniculatus* decreased. Sunshine duration was lowest in vacant QUARRY, differing from the three other habitat types. Since vegetation structure and sunshine duration strongly differed among the habitat types, temperature in the microhabitats did so too (Fig. 2). During daytime, temperatures decreased from occupied QUARRY to vacant GRASS to vacant QUARRY. Occupied GRASS had an intermediate position. At night-time, the pattern was similar, however, only occupied QUARRY differed from vacant QUARRY.

The GLMM analysis identified macroclimate, landscape quality and habitat quality as drivers of patch occupancy of *P. argus* (Table 3). In the macroclimate model, patch occupancy of *P. argus* decreased with temperature. The landscape-quality model revealed a positive relationship between connectivity of the patches and patch occupancy. In the habitat-quality model, the occurrence of the species was best predicted by the cover of the host plant, *L. corniculatus*. In the synthesis model, the cover of the host plant remained as the only predictor variable (Table 3, Fig. 3). For all models, the explanatory power and the discriminative ability was high (R^2_{GLMMm} 0.35–0.87, AUC 0.89–0.97).

Abundance

Mean abundance of adult *P. argus* was nearly four times higher at occupied QUARRY than at occupied GRASS (Fig. 4). The GLMM analysis detected habitat quality as the driver of *P. argus* adult abundance (Table 4). In contrast, macroclimate and landscape quality had no effect on butterfly abundance. In both the habitat-quality and the synthesis model, the abundance of the species was best predicted by the cover of the host plant, *L. corniculatus*, the cover of bedrock as well as a low vegetation density (Table 4; Fig. 5). Again, the explanatory power of the models was high (R^2_{GLMMm} 0.37–0.41).

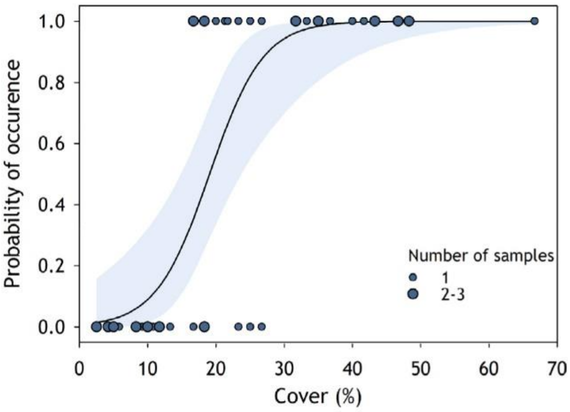

Fig 3. Relationship between patch occupancy of *Plebejus argus* and the significant parameter (cover of the host plant *L. corniculatus*) of the averaged synthesis model. The regression slope (including 95% confidence intervals) was fitted by using single predictor GLMM with binomial error structure (see Table 3): $y = 1/(1 + \exp(-(-4.87718 + 0.25596 \times L.\ corniculatus)))$, $P < 0.01$, $R^2_{GLMMm} = 0.80$, $R^2_{GLMMc} = 0.80$. R^2_{GLMMm} = variance explained by fixed effects, R^2_{GLMMc} = variance explained by both fixed and random effects (Nakagawa *et al*., 2017).

Discussion

Our study revealed that limestone quarries are the most important refuge for the formerly widespread Silver-studded Blue. Originally, *P. argus* was common in calcareous grasslands across the study area (Retzlaff, 1973; Fartmann, 2004). More recently, however, patch occupancy was five times higher at quarries compared to calcareous grasslands and mean adult abundance nearly four times higher at occupied quarries than at occupied grasslands. Active management favoured the occurrence of *P. argus* in quarries and was even an essential prerequisite in calcareous grasslands. The key driver of patch occupancy and adult abundance in the synthesis models was a high abundance of the host plant. Adult abundance, additionally, increased with a sparse vegetation and a high cover of bedrock.

Macroclimate is an important predictor of butterfly distribution (Settele *et al*., 2008; Chen *et al*., 2011; Devictor *et al*., 2012). This has also been documented for many species across the elevational gradient of the study area (Fartmann, 2004; Stuhldreher & Fartmann, 2018). In our study, we detected a negative relationship between patch occupancy of *P. argus* and temperature in the macroclimate GLMM. Occupied patches situated at higher elevations were characterised by more frost days, higher precipitation and lower temperatures than vacant patches. However, it is unlikely that the observed patterns reflect a genuine preference for cool and wet climates. In fact, we attribute these relationships by the predominant occurrence of the main habitat, limestone quarries, especially those

Table 3. Statistics of GLMM: Relationship between patch occupancy of *Plebejus argus* [binomial response variable: Occupied ($n = 29$) versus vacant patches ($n = 22$)] and several environmental parameters (metric predictor variables). 'Habitat type' and 'subarea' were used as random factors. Model-averaged coefficients (conditional average) were derived from the top-ranked models (ΔAICC < 3).

Parameters	Estimate	SE	Z	*P*	R^2_{GLMMm}	R^2_{GLMMc}	AUC
(a) Macroclimate					0.35	0.46	0.89
(Intercept)	34.52	12.60	2.74	*			
Temperature	−3.63	1.33	−2.74	*			
(b) Landscape quality					0.72–0.77	0.75–0.79	0.94
(Intercept)	6.53	2.64	2.42	*			
Connectivity	0.85	0.30	2.78	**			
Not significant: patch size							
(c) Habitat quality					0.84–0.87	0.87–0.89	0.97
(Intercept)	−5.15	3.49	1.45	n.s.			
Lotus corniculatus	0.27	0.09	2.76	**			
Not significant: sunshine, vegetation density, bare ground, bedrock, small shrubs, herbs							
(d) Synthesis model					0.80–0.83	0.82–0.85	0.96
(Intercept)	14.82	15.45	0.95	n.s.			
Lotus corniculatus	0.24	0.08	2.70	**			
Not significant: temperature, connectivity							

R^2_{GLMMm} = variance explained by fixed effects, R^2_{GLMMc} = variance explained by both fixed and random effects (Nakagawa *et al*., 2017), AUC = area under the curve; accuracy of model prediction (Fielding & Bell, 1997). Significance levels are indicated as follows: *n.s.* not significant, *$P < 0.05$, **$P < 0.01$.

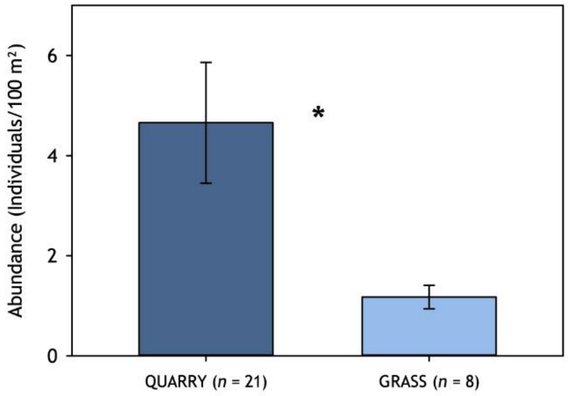

Fig 4. Mean (±SE) abundance of *Plebejus argus* in occupied QUARRY ($n = 21$) and occupied GRASS ($n = 8$). Differences between the two groups were tested using GLMM, see 'Statistical analysis' section for details; $^{*}P < 0.05$.

with active management, in the highest elevations of the study area (cf. 'Study area' section). In line with this, *P. argus* is known to occur across very different macroclimates throughout Europe (Nunner, 2013; Meineke, 2020) and is even considered a thermophilous species (Asher *et al.*, 2001).

Recent studies have shown that the distribution of habitat-specialist butterflies in cultivated landscapes is mainly driven by (i) habitat quality within patches, (ii) patch size and (iii) patch connectivity (Eichel & Fartmann, 2008; Stuhldreher & Fartmann, 2014; Poniatowski *et al.*, 2018b). The relative importance of these factors, however, depends on the mobility of the species, its population structure and the landscape composition (Dover & Settele, 2009; Stuhldreher & Fartmann, 2014; Münsch *et al.*, 2019). Nonetheless, habitat quality is considered the most important predictor of species survival in fragmented landscapes (Poniatowski *et al.*, 2018b).

Patch size did not affect patch occupancy and abundance in our study. *Plebejus argus* is an extremely sedentary butterfly species (Thomas & Harrison, 1992; Lewis *et al.*, 1997) and colonised patches are often small. In British calcareous grasslands, patch size varied mainly between 0.1 and 5 ha (Thomas, 1985b; Thomas *et al.*, 1992). In our study, occupied patches were also tiny and had a mean size of 1.0 (quarries) and 0.8 ha (calcareous grasslands). In contrast, unoccupied quarries with no information about a former occurrence of *P. argus* were much larger (mean size: 6.1 ha) but more isolated (mean patch connectivity: 4.1 km). Consequently, we assume that *P. argus* is able to persist in fairly small habitats if further patches occur in close proximity or habitat quality is high (cf. Münsch *et al.*, 2019). Indeed, patch occupancy increased in the landscape-quality model with connectivity.

However, habitat quality was the most important driver of patch occupancy and adult abundance. A high cover of the host plant *L. corniculatus* favoured both patch occupancy and butterfly abundance. Additionally, abundance of *P. argus* increased with early-successional stages, i.e. sparse vegetation and a high cover of bedrock. Sufficient food is of vital importance for successful development of the larvae. Consequently, a high abundance of host plants is known to determine habitat quality in many butterfly species (García-Barros & Fartmann, 2009; Curtis *et al.*, 2015).

Vegetation structure is usually interrelated with microclimate (Stoutjesdijk & Barkman, 1992). Early-successional stages characterised by a sparse vegetation and high cover of bedrock favour a warm microclimate, which is preferred by various butterfly species in general (García-Barros & Fartmann, 2009; Dennis, 2010) and *P. argus* in particular (Thomas, 1985b; Jordano *et al.*, 1992; Hodgson *et al.*, 2015) for oviposition. In

Table 4. Statistics of GLMM: Relationship between the abundance of *Plebejus argus* at occupied patches [negative-binomial response variable: Individuals/100 m^2 ($n = 29$)] and several environmental parameters (metric predictor variables). 'Habitat type' and 'subarea' were used as random factors. Model-averaged coefficients (conditional average) were derived from the top-ranked models (ΔAICC < 3).

Parameter	Estimate	SE	Z	*P*	R^2_{GLMMm}	R^2_{GLMMc}
(a) Macroclimate						
Not significant: temperature						
(b) Landscape quality						
Not significant: connectivity, patch size						
(c) Habitat quality					0.37–0.41	0.37–0.41
(Intercept)	0.34	0.52	0.65	n.s.		
Lotus corniculatus	0.03	0.01	3.06	**		
Bedrock	0.02	0.01	1.97	*		
Vegetation density	−0.02	0.01	2.08	*		
Not significant: sunshine, vegetation height, bare ground, small shrubs, herbs						
(d) Synthesis model					0.37–0.41	0.37–0.41
(Intercept)	0.33	0.57	0.56	n.s.		
Lotus corniculatus	0.03	0.01	2.95	**		
Bedrock	0.02	0.01	2.08	*		
Vegetation density	−0.01	0.01	2.09	*		

R^2_{GLMMm} = variance explained by fixed effects, R^2_{GLMMc} = variance explained by both fixed and random effects (Nakagawa *et al.*, 2017). Significance levels are indicated as follows: *n.s.* not significant, $^{*}P < 0.05$, $^{**}P < 0.01$.

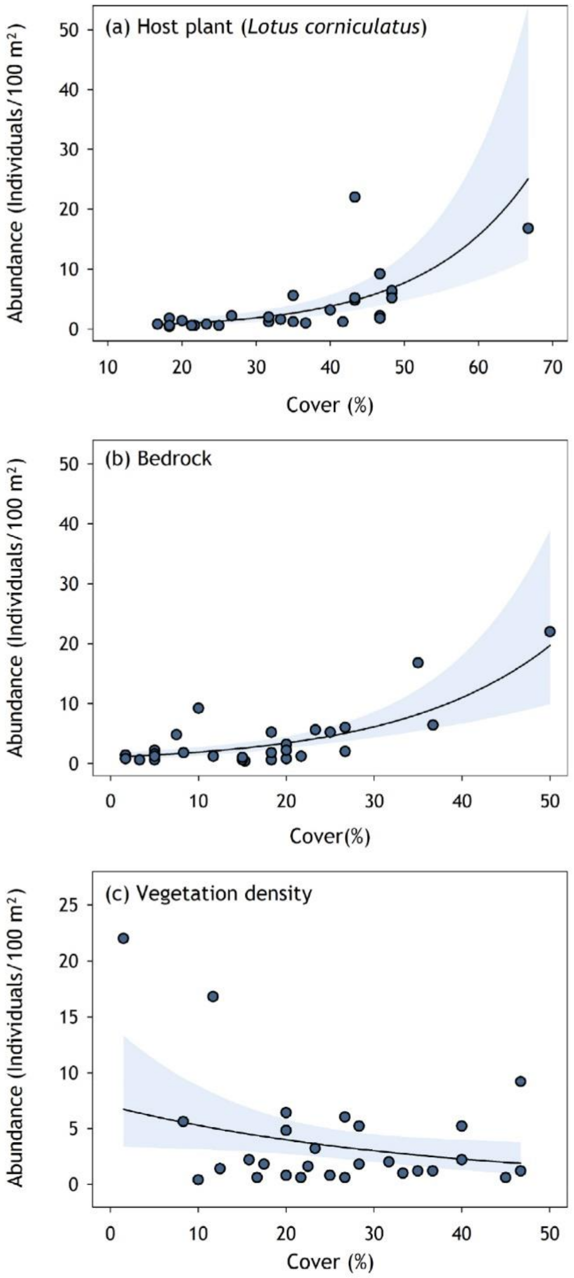

Fig 5. Relationship between abundance of *Plebejus argus* and the significant parameters of the averaged synthesis model. The regression slopes (including 95% confidence intervals) were fitted by using single predictor GLMM with negative-binomial error structure (see Table 4): (a) $y = \exp(-1.47512 + 0.07043 \times L.\ corniculatus)$, $P < 0.001$, $R^2_{GLMMm} = 0.60$, $R^2_{GLMMc} = 0.63$; (b) $y = \exp(0.06747 + 0.05826 \times \text{bedrock})$, $P < 0.01$, $R^2_{GLMMm} = 0.38$, $R^2_{GLMMc} = 0.40$; (c) $y = \exp(1.94455–0.02811 \times \text{vegetation density})$, $P < 0.05$, $R^2_{GLMMm} = 0.14$, $R^2_{GLMMc} = 0.14$. R^2_{GLMMm} = variance explained by fixed effects, R^2_{GLMMc} = variance explained by both fixed and random effects (Nakagawa *et al*., 2017).

accordance with this, occupied quarries and grasslands were characterised by higher temperatures during daytime compared to vacant quarries. Additionally, occupied quarries were also warmer than vacant grasslands. Besides the immature stages of *P. argus*, the host ants also depend on high ambient temperatures. On calcareous soils, *Lasius alienus* is usually the main host (Jordano *et al*., 1992; Jordano & Thomas, 1992). This ant species is thermophilous and its nest density increases with shallow, skeletal soils (Jordano *et al*., 1992; Seifert, 2018). Such soil conditions also foster the colonisation of the host plant, *L. corniculatus* (Grime *et al*., 2007).

In recent decades, *P. argus* has strongly declined in calcareous grasslands of the study area (Fartmann, 2004), although large and well-connected calcareous grasslands with occurrence of *L. corniculatus* are still common (Fartmann, 2004; Poniatowski *et al*., 2018a, 2018b). Dense stands of *L. corniculatus*, however, are rare today in these grasslands (Fartmann, 2004). Most of these calcareous grasslands have suffered from abandonment or a decreasing grazing intensity (Fartmann, 2004) favouring competitive, dense-growing grasses (e.g. *Brachypodium pinnatum*, *Bromus erectus*) at the expanse of poor competitors such as *L. corniculatus* (Grime *et al*., 2007; Poniatowski *et al*., 2018a). In line with this, the few remaining calcareous grasslands with occurrence of *P. argus* were all managed ones. The influence of atmospheric nitrogen deposition possibly also contributes to the deterioration of habitat quality in calcareous grasslands. In nutrient-poor habitats on deeper soils eutrophication promotes the establishment of taller vegetation, resulting in microclimatic cooling (Wallis de Vries & van Swaay, 2006; Roth et al., 2021).

In contrast, limestone quarries still host abundant populations of *P. argus* in the study area. We explain the higher patch occupancy and adult abundance in quarries especially by a more favourable habitat quality. Occupied quarries had a much higher cover of *L. corniculatus* and bedrock than occupied calcareous grasslands. In quarries still used for mining, early-successional stages rich in *L. corniculatus* as well as gravel, stones or rocks having a warm microclimate regularly emerge (own observation). Additionally, and in contrast to calcareous grasslands, quarries are characterised by a very low successional speed due to the shallow soils, even without further management after abandonment of mining (Poschlod *et al*., 1997, Tropek *et al*., 2010). Hence, they are characterised by a suitable habitat quality for much longer time periods than abandoned calcareous grasslands, which are strongly dependent on regular management. In accordance with this, *P. argus* has only disappeared from rather small (mean size: 1.4 ha) and isolated (mean patch connectivity: 4.8 km) quarries and those that have been abandoned for more than 50 years (own observations). Here, the invasion of woody plants (e.g. *Salix caprea*, *Prunus spinosa*, *Rhamnus cathartica*, *Crataegus* spp.) has led to strong shading of the herb layer (own observation) and, thus, to an adverse microclimate.

In conclusion, the deterioration of habitat quality due to abandonment and decreasing grazing intensity has resulted in a strong decline of *P. argus* in calcareous grasslands of the study area. Today, limestone quarries, especially those being actively managed, are the most important refuges for the species. Quarries exhibit a very low successional speed due to their shallow soils. Hence, they are characterised by a high habitat quality for *P. argus*, i.e. dense stands of the host plant *L. corniculatus*, which grow on skeletal soils providing warm microclimatic conditions.

Implications for conservation

Preserving limestone quarries with their early-successional stages is of crucial importance for the conservation of *P. argus*. Hence, in abandoned quarries, technical reclamation including backfilling and afforestation has to be prevented (Tropek *et al*., 2010). Although quarries are characterised by a very low successional speed (cf. 'Discussion' section), trees and shrubs have to be removed periodically to avoid shading (Poschlod *et al*., 1997). In particular in old abandoned quarries where thicker soil layers have developed, topsoil removal is important to re-create early-successional stages (Konvička & Fric, 2002). The positive effects of topsoil removal in quarries on *P. argus* colonies have already been documented by De Whalley *et al*. (2006). In their study, the cover of *L. corniculatus* increased, the host ant *L. alienus* recolonised the restoration sites and the abundance of adult *P. argus* also flourished.

In calcareous grasslands, we recommend the reintroduction of regular, rough grazing with sheep and goats. Such a grazing regime creates habitat heterogeneity and fosters the expansion of early-successional stages (Wallis de Vries *et al*., 2002; Eichel & Fartmann, 2008). Especially, grazing in winter and spring seems to be suitable to favour both the host plant and *P. argus*. *Lotus corniculatus* regenerates mainly by seeds and usually germinates in spring (Grime *et al*., 2007). Indeed, Goodenough and Sharp (2016) detected a strong positive relationship between grazing in spring and the cover of *L. corniculatus* in British calcareous grasslands. In our study area, half of the calcareous grasslands currently unoccupied by *P. argus* are still managed, but not all grasslands are grazed multiple times every year. This implies that the intensity and seasonal time interval of the present grazing regime does not favour the habitat demands of our target species. Therefore, we suggest that the intensification of the management regime of these grasslands should be adjusted at least partly.

Additionally, maintaining a dense network of suitable habitat patches appears to be crucial for the species' persistence in fragmented landscapes (Lewis *et al*., 1997; this study). Lewis *et al*. (1997) showed that the proportion of *P. argus* individuals migrating between habitat patches is generally low and that the probability of migration does increase with population density. Therefore, conservation management should focus on quarries and calcareous grasslands inhabiting large populations. Additionally, stepping stones should be restored in close vicinity (mean distance to the next three occupied patches ≤ 2 km) between these large core populations (Thomas & Harrison, 1992; Lewis *et al*., 1997; this study). Currently unoccupied patches with no historical data about a former patch occupancy but providing suitable habitat conditions should be particularly included in this network.

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Conflict of interest

The authors declare that they have no conflict of interest.

Data Availability Statement

Data are available on request from the authors.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 Absolute and relative frequencies of the nominal variables 'habitat type' and 'land use' at occupied, vacant and unoccupied patches of *Plebejus argus*. Differences in absolute frequencies between habitat types were analysed with Fisher's exact test. Significance levels are indicated as follows: *n.s.* not significant, $*P < 0.05$, $***P < 0.001$.

Table S2 Mean values (± SE) of macroclimatic and landscape parameters at the six habitat types. Differences among habitat types were analysed by LMM/GLMM and subsequent Tukey contrasts, see materials and methods for details. Habitat types without consistent letters indicate significant differences ($P < 0.05$). Significant differences between the habitat types are also indicated by bold type. Significance levels are indicated as follows: *n.s.* not significant, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

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Active management fosters species richness of wild bees in limestone quarries

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Abstract

Open and unreclaimed quarries often host species-rich plant and animal communities. However, the specific factors that determine biodiversity in such anthropogenic habitats are largely unknown. This applies in particular to diverse groups of insects. We therefore studied bee assemblages of 16 limestone quarries, eight active and eight abandoned ones, in a Central European landscape with a long history of quarrying. We analysed the influence of macroclimate, landscape quality and habitat quality on overall species richness as well as on the number of threatened and oligolectic species. Our study revealed strong differences in habitat quality and composition of bee assemblages between active and abandoned quarries. Active quarries were larger, had more different pollen sources and a higher cover of early but a lower cover of later successional stages than abandoned quarries. As a result, species richness of bees was higher in active compared to abandoned quarries. Additionally, active quarries were characterized by a unique bee assemblage consisting of several indicator species. Availability of pollen sources and nesting habitats predicted bee species richness in the quarries. Overall, habitat quality and composition of bee assemblages were strongly dependent on quarry management. Active mining continuously created early-successional stages rich in pollen sources and sunlit nesting habitats, favouring species richness of bees in general and of threatened and oligolectic species in particular. Successional speed is generally low in quarries. Nevertheless, in abandoned quarries, later successional stages increasingly dominated due to ongoing succession and, hence, habitat quality and species richness of bees decreased. Considering this, we propose to expand existing quarries rather than build new ones. From a conservation point of view, this approach has several advantages: (i) existing quarries are often already refuges for colonies of rare species; (ii) many species of conservation concern have a low mobility and are therefore unable to occupy remote habitats and (iii) in the impoverished modern-day landscapes, source population that may colonize new quarries are often lacking.

Key words: Biodiversity conservation; habitat quality; insect decline; mining site; pollinator community; successional gradient

1. Introduction

Semi-natural habitats, such as nutrient-poor grasslands, are hotspots of biodiversity (Feurdean et al., 2018; Hooftman et al., 2021). However, since the second half of the 19th century, they have suffered severe habitat loss, in particular due to land-use change (Foley et al., 2005; Stoate et al., 2009). The habitat depletion has led to a dramatic erosion of biodiversity in general and decrease of insects in particular (Cardoso et al., 2020; Sánchez-Bayo and Wyckhuys, 2019; Wagner, 2020). Today, the remaining semi-natural habitats are often islands in an intensively managed agricultural landscape (Deák et al., 2021; Poniatowski et al., 2018). To counteract the ongoing loss of insect diversity, the maintenance of these habitat remnants is of crucial importance (Samways et al., 2020). Moreover, secondary habitats may also contribute to biodiversity conservation in such landscapes (Gueth et al., 2021; Heneberg et al., 2018; Kaur et al., 2019; Torma et al., 2018).

A prominent example therefor are quarries (Beneš et al., 2003; Münsch and Fartmann, 2022; Prach et al., 2014; Tropek et al., 2010; Tropek and Konvička, 2008). For a long time, they had a negative image among conservationists and were considered to be scars in the landscape (Beneš et al., 2003). Indeed, quarrying results in fundamental changes of the environmental conditions and landscape, since existing vegetation and top soil are removed (Bétard, 2013; Kalarus et al., 2019). After abandonment of mining, quarries were often reclaimed and afforested (Krauss et al., 2009; Tropek et al., 2010). However, by now, it has been proven that open and unreclaimed quarries often host species-rich plant and animal communities (Beneš et al., 2003; Řehounková et al., 2020; Šálek, 2012; Tropek et al., 2010). Many quarries are characterized by sparsely-vegetated early-successional stages providing warm microclimatic conditions. Hence, quarries may become important habitats for xero-thermophilous and commonly threatened habitat specialists (Beneš et al., 2003; Münsch and Fartmann, 2022; Tropek and Konvicka, 2008). Such species have frequently disappeared from modern-day agricultural landscapes since early-successional stages rich in bare soil (i) have vanished as a result of habitat loss and (ii) rapidly become overgrown due to the general eutrophication of the soils (Nijssen et al., 2017). By contrast, successional speed in quarries is low due to the lack of topsoil and otherwise shallow soil (Gilcher and Tränkle, 2005; Münsch and Fartmann, 2022; Prach et al., 2011, 2014). So far, there is a gap of knowledge as to whether active quarries can be as important for biodiversity conservation as abandoned ones (though regarding for butterflies see Beneš et al., 2003; Münsch and Fartmann, 2022).

In our study, we chose wild bees (hereinafter termed 'bees') as a model system. Bees are of great functional importance as pollinators for wild and crop plants (Klein et al., 2007; Mathiasson and Rehan, 2020; Waser and Ollerton, 2006; Winfree et al., 2008). The main predictors of species richness of bees are the diversity of pollen sources (Holzschuh et al., 2008; Roulston and Goodell, 2011; Twerd and Banaszak-Cibicka, 2019) and availability of suitable nesting sites (Potts et al., 2005; Westrich, 2018). Overall, bees are excellent indicators of environmental conditions (Nielsen et al., 2011; Westphal et al., 2008). This is especially true for characteristics at the habitat level since bees are rather sedentary and usually have a small home range (Gathmann and Tscharntke, 2002).

In this paper, we studied the bee assemblages of 16 randomly selected limestone quarries, eight active and eight abandoned ones, in a Central European landscape with a long history of quarrying. We analysed the influence of macroclimate, landscape quality and habitat quality on overall species richness as well as on the number of threatened and oligolectic species. Based on our results, we give management recommendations that favour biodiversity in quarries across Central Europe.

2. Material and methods

2.1. Study area

The study was carried out in central Germany, in the eastern part of the German Federal State of North Rhine-Westphalia. The study area covered approximately 2.800 km^2 and was divided into four subareas: (i) Teutoburger Wald, (ii) Lippisches Bergland, (iii) Hellweg and (iv) Oberwälder Land (Fig. 1). The climate is suboceanic with a mean annual temperature of 9.5 °C and a mean annual precipitation of 951 mm (meteorological station Bad Lippspringe [157 m a.s.l]; period: 1981–2010; DWD, 2021). The subareas Lippisches Bergland and Oberwälder Land comprise wooded hills and ridges as well as wide valleys mainly covered by grasslands. The subareas Hellweg and Teutoburger Wald are located at the southeastern and northeastern edge of the Westphalian Basin, respectively, which is dominated by agriculture. Quarrying is a century-old tradition in the study area. The limestone is mined in quarries and used for the production of gravel, bricks, building material or cement.

2.2. Study plots

Within the study area, a total of 16 limestone quarries, eight active and eight abandoned ones, were randomly selected (Fig. 1 and 2). Quarry size varied between 6 and 98 ha (mean: 33 ha ± 8 SE).

2.3. Environmental conditions

For each quarry, we sampled environmental parameters of (i) macroclimate, (ii) landscape quality and (iii) habitat quality (Table 1). Climate data were obtained from 1-km² grid datasets of Germany's National Meteorological Service (DWD, 2021). For our analyses, we considered average annual temperature (°C) and precipitation (mm) (long-term mean: 1981–2010). Mean elevation (m a.s.l.) and latitude of the quarries was taken from topographic maps by using the geographical information system ArcGIS 10.3.1.

To assess landscape quality, we differentiated four coarse land-use types: arable land, grassland, forest and urban area (Table 1). We calculated their cover in a radius of 200 m around each quarry by using aerial photographs with ArcGIS 10.3.1.

Habitat types, density of open earthen banks/scarps (m/10 ha) (Fig. 2a) as the most important breeding habitat of Central European bees (cf. Westrich, 2018) and quarry size were mapped in September 2019 for each quarry using aerial photographs and subsequently digitized in ArcGIS 10.3.1 (Table 1). Based on vegetation and habitat structure, we differentiated a maximum of eleven habitat types: unvegetated (bare ground, gravel or stones), annual and perennial ruderal vegetation, mesic grasslands, calcareous grassland with and without shrubs, shrubberies, fringes and forests. The number and proportion of the habitat types per quarry were used to calculate the Shannon index as a measure of habitat heterogeneity (Krauss et al., 2009; Helbing et al., 2017). All flowering plant species that are considered as potential pollen sources for oligolectic bee species according to Westrich (2018) were counted. All of these plants are also exploited by at least some polylectic species (cf. Westrich, 2018). During each survey, all habitat types within the respective quarry were visited and the plant species were noted within one hour. We used the sum of the different detected plant species across all eight surveys ('no. of pollen sources') as an explanatory variable. For abandoned quarries, we additionally ascertained the year of the last mining activity as a measure for the effects of succession by interviewing the land owners.

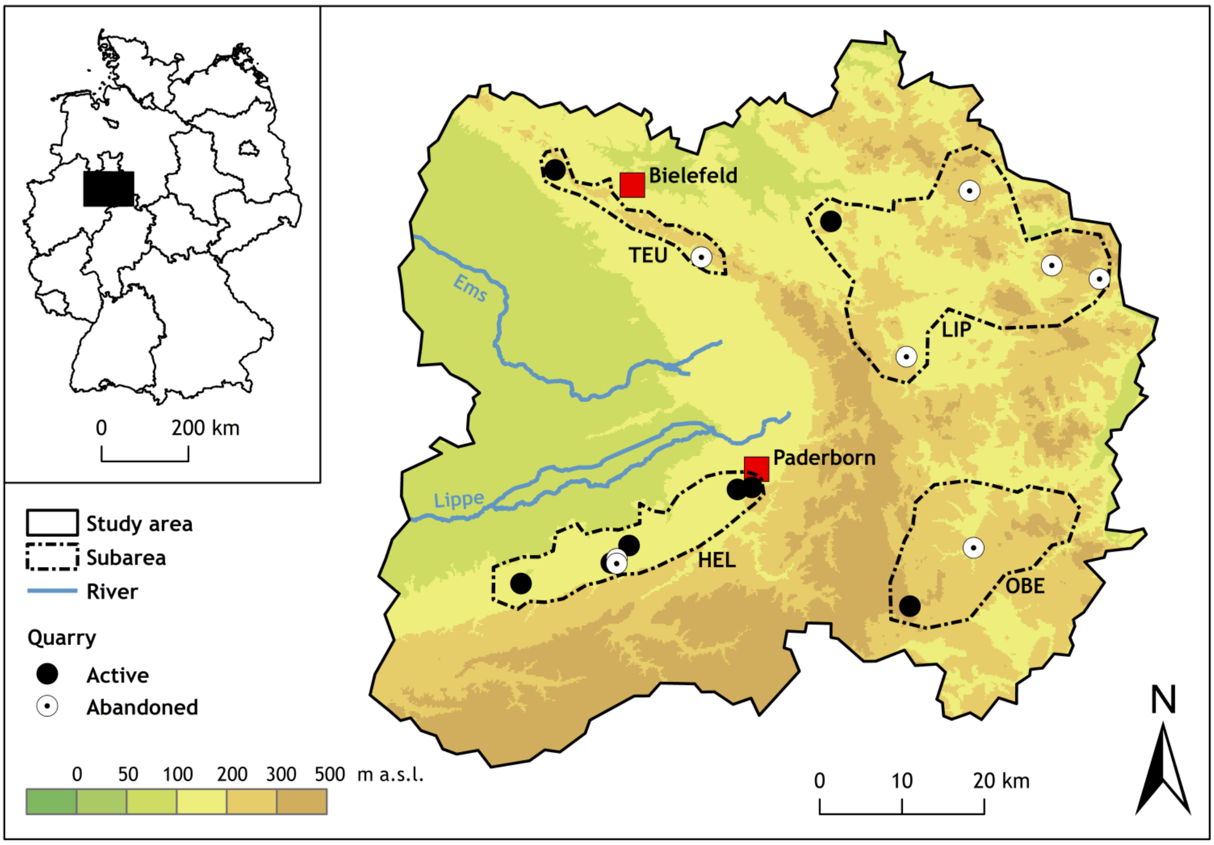

Figure 1 The study area in the eastern part of North Rhine-Westphalia in central Germany (inlay) and the location of the four subareas Teutoburger Wald (TEU), Lippisches Bergland (LIP), Hellweg (HEL) and Oberwälder Land (OBE) with plots (active and abandoned limestone quarries).

2.4. Bee sampling

Bee assemblages were sampled by using the variable transect method (Nielsen et al., 2011; Westphal et al., 2008) from late March to early September 2019. Each quarry was visited eight times with an interval of/ three weeks between each survey. During a standardized period of two hours, we controlled all potential bee resources (flowers, nesting structures) per quarry under favourable weather conditions (sunny and calm, minimum air temperature: 15 °C) from 10 am to 5 pm. Detected bees were collected by using an insect net. Species identifiable in the field were released after determination. All other individuals were killed with ethyl acetate and identified in the lab by using binoculars. Bees were determined to species level according to the identification keys mentioned in Appendix A. For statistical analysis, we classified three groups of bees: all, oligolectic (according to Westrich, 2018) and threatened species (according to the red data book of North Rhine-Westphalia [Esser et al., 2010]; including near threatened species).

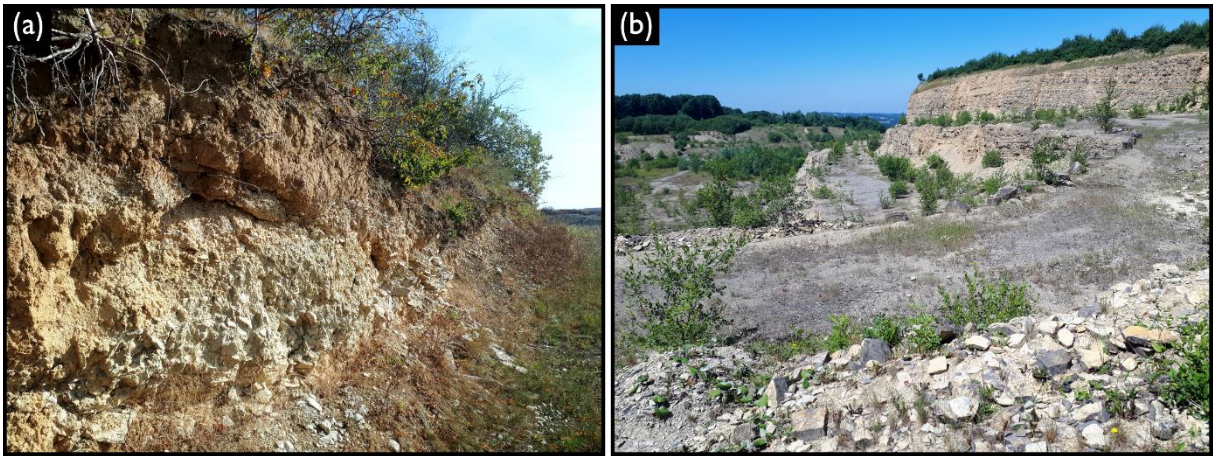

Figure 2 (a) Example of an earthen bank within a limestone quarry. Such habitat structures offer valuable nesting opportunities for numerous bee species (Westrich, 2018); (b) overview of an abandoned limestone quarry in the study area (Photos: M. Kettermann).

2.5. Statistical analysis

All statistical analyses were performed using R 4.4.1 (R Development Core Team, 2021). Generalised Linear Mixed-effects Models (GLMM) were fitted with 'subarea' (see Section 2.1) as a random intercept (*lme4* package; Bates et al., 2021). The environmental parameters (see Section 2.3) as well as the number of all, threatened and oligolectic bee species (see Section 2.4) were compared between both quarry types by univariable GLMMs. Depending on the distribution of the response variable, GLMMs with negative-binomial or Poisson error structure, respectively, were applied. The significance of the predictor variable was assessed with likelihood-ratio tests (Type III tests).

To identify species that were characteristic either of active or abandoned limestone quarries, an Indicator Species Analysis (ISA) was carried out using the 'multipatt' function in the package 'indicspecies' (de Cáceres and Legendre, 2009) and the association index "IndVal.g" (de Cáceres et al., 2010). The statistical significance of the indicator values was tested by a permutation test with 9,999 permutations (de Cáceres and Legendre, 2009).

To analyse which environmental parameters (see Section 2.3) explained species richness of all, threatened and oligolectic bees (see Section 2.4) within the quarries ($N = 16$), we conducted multivariable GLMMs. In a preparatory step, prior to the analyses, we tested all predictor variables for multicollinearity. If two or more variables were strongly intercorrelated (Pearson correlation [r], $|r| > 0.6$, $P < 0.05$), just one—the ecologically comprehensible variable—was used for statistical modelling (e.g. Helbing et al., 2021; Table B1, Appendix B). To avoid model overfitting, the analysis was performed in two steps: initially, univariable GLMMs were fitted for all combinations of response and predictor variables in order to detect which predictor variables had an impact on the given response variable (likelihood-ratio tests, $P < 0.05$) (Table B2, Appendix B). In a second step, the multivariable models were calculated for all, threatened and oligolectic bee species with the previously determined predictor variables. In order to identify the most relevant environmental parameters and their relative importance (RI) within our multivariable models, we applied model averaging based on an information-theoretic approach (Grueber et al., 2011). Model averaging was conducted using the 'dredge' function (package MuMIn; Bartón, 2019) and only included top-ranked models within $\Delta AIC_C < 3$ (cf. Grueber et al., 2011).

To assess the effects of succession within abandoned quarries, we tested whether there was a relationship between the variable 'years since last mining' (see Section 2.2) and the three response variables (species richness of all, threatened and oligolectic bees) within abandoned quarries. Therefore, we conducted three univariable GLMMs with a Poisson error structure. We evaluated the explanatory power of all models by calculating marginal (variance explained by fixed effects) and conditional analysis (variance explained by both fixed and random effects) R^2 (Nakagawa et al., 2017).

3. Results

3.1. Environmental conditions

Macroclimate and landscape quality did not differ between the two quarry types (Table 1). The only exception was the cover of urban area in the surrounding of the quarries, which was higher around active quarries. By contrast, habitat quality differed considerably between active and abandoned quarries. Active quarries were larger, had more different pollen sources and a higher cover of early-successional stages (unvegetated, perennial ruderal vegetation) but a lower cover of later successional stages (calcareous grasslands with shrubs, shrubberies, forests) than abandoned quarries. All other parameters of habitat quality did not differ between the two types of quarries. The last mining activity in abandoned quarries took place 12 to 86 years ago (mean: 39 ± 13 SE).

3.2. Bee species assemblages and response to environmental conditions

In total, we detected 159 bee species in the 16 quarries (Table B3, Appendix B). Among them were 44 threatened (28%) and 35 oligolectic species (22%). Species richness of bees (all, threatened and oligolectic species) was higher in active compared to abandoned quarries (Fig. 3).

Active quarries were characterized by a unique bee assemblage. The ISA identified six species indicative for active quarries, among them one threatened species (*Osmia adunca*) (Table 2). By contrast, abandoned quarries had no indicator species.

Table 1 Overview of environmental parameters (mean ± SE, minimum and maximum). Differences in environmental parameters between active (N = 8) and abandoned limestone quarries (N = 8) were analysed using Generalized Linear Mixed-effects Models (Poisson error structure) with ‘subarea’ as a random intercept (for details see Section 2.5). Statistical significance is indicated as follows: n.s. = not significant; $P \geq 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Parameter	**ACTIVE**		**ABANDONED**		***P***
	Mean (± SE)	Min.-Max.	Mean (± SE)	Min.-Max.	
Macroclimate					
Elevation (m a.s.l.)	163 ± 21	108–289	208 ± 18	151–310	n.s.
Latitude	8.7 ± 0.1	8–9	9.0 ± 0.1	9–9	n.s.
Mean annual precipitation (mm)	917 ± 29	830–1072	915 ± 35	815–1088	n.s.
Mean annual temperature (°C)	9.2 ± 0.2	8–10	9.1 ± 0.1	9–10	n.s.
Landscape quality*					
Arable land (%)	34.0 ± 8.0	11–67	27.1 ± 10.2	0–73	n.s.
Grassland (%)	10.4 ± 3.0	1–29	20.8 ± 8.2	0–75	n.s.
Forest (%)	34.1 ± 7.0	9–55	48.0 ± 8.7	18–88	n.s.
Urban area (%)	15.9 ± 4.3	2–38	4.5 ± 3.7	0–30	*
Habitat quality					
Habitat types (%)					
Unvegetated	29.3 ± 5.6	6–59	0.4 ± 0.4	0–3	***
Annual ruderal vegetation	29.6 ± 4.5	15–57	24.5 ± 6.9	0–56	n.s.
Perennial ruderal vegetation	6.8 ± 2.4	1–21	1.0 ± 0.5	0–4	**
Mesic grassland	1.3 ± 0.6	0–4	2.1 ± 1.5	7–13	n.s.
Calcareous grassland without shrubs	6.2 ± 1.7	2–17	10.1 ± 4.5	0–40	n.s.
Calcareous grassland with shrubs	4.0 ± 1.6	0–13	15.7 ± 3.9	7–40	**
Shrubbery	13.7 ± 2.1	7–23	22.2 ± 2.2	16–30	**
Fringe	1.8 ± 0.5	0–4	2.1 ± 0.8	0–5	n.s.
Forest	4.2 ± 1.4	0–10	21.3 ± 6.0	0–55	**
Habitat heterogeneity (Shannon index)	1.6 ± 0.1	1–2	1.5 ± 0.1	1–2	n.s.
Density earthen banks/scarps (m/10ha)	1.6 ± 0.4	0.4–3.9	1.5 ± 0.4	0.0–3.3	n.s.
No. pollen sources (plant species)	68.0 ± 2.5	57–80	47.3 ± 6.5	17–64	***
Quarry size (ha)	52.6 ± 11.1	15–98	14.1 ± 4.2	6–35	**

* Cover of land-use types (%) within a radius of 200 m around each quarry.

Availability of pollen sources was the most important predictor of species richness of bees in quarries (Table 3, Fig. 4). The number of bee species (all, threatened and oligolectic species) increased with the number of different pollen sources. Availability of pollen sources was negatively correlated with the cover of calcareous grasslands with shrubs and positively with the cover of annual ruderal vegetation (Table B1, Appendix B). Sufficient nesting habitats were also important for species-rich bee assemblages. A high density of open earthen banks/scarps favoured the number of all and threatened bee species (Table 3, Fig. 4). Additionally, the overall number of bee species increased with the cover of unvegetated area, which was positively correlated with quarry size but negatively with shrubberies (Table B1, Appendix B). The explanatory power of the GLMMs was very high (R^2_m = 0.64–0.90; R^2_c = 0.64–0.92).

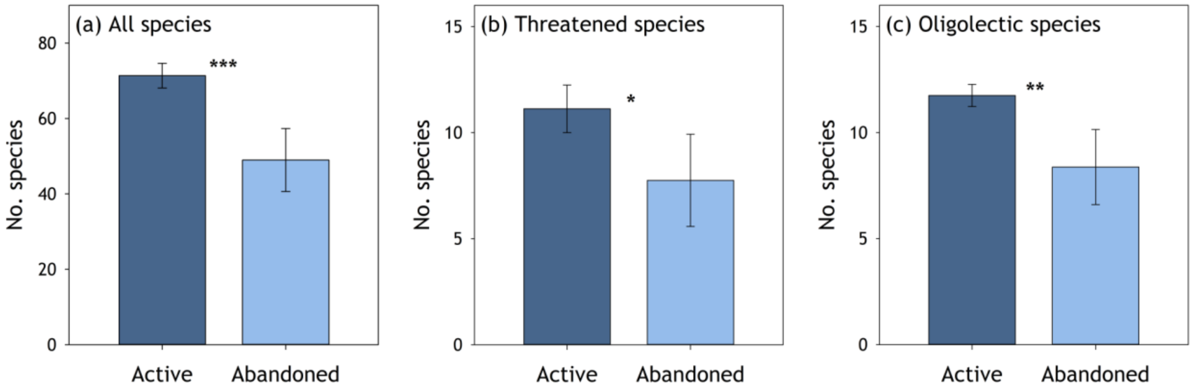

Figure 3 Mean (± SE) species richness of all (a), threatened (b) and oligolectic bee species (c) in active (N = 8) and abandoned limestone quarries (N = 8). Differences in species richness between quarry types were analysed using Generalized Linear Mixed-effects Models (Poisson error structure) with 'subarea' as a random intercept (for details see Section 2.5). Statistical significance is indicated as follows: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 2 Results of indicator species analysis: Bee indicator species of active ($N = 8$) and abandoned limestone quarries ($N = 8$). Species are sorted by their indicator values (VI). Only species with significant IVs are shown. Threatened species are highlighted by bold type. A list of all species is provided in table A1 (Appendix A). % = frequency. Statistical significance is indicated as follows: * $P < 0.05$; ** $P < 0.01$.

Indicator species	**Quarry type**				***P***
	Active		Abandoned		
	IV	%	IV	%	
Andrena gravida	89	100.0	.	25.0	**
Hylaeus gredleri	88	87.5	.	12.5	**
Hylaeus signatus	85	100.0	.	37.5	*
Lasioglossum calceatum	85	100.0	.	37.5	*
Osmia adunca	80	75.0	.	12.5	*
Sphecodes geofrellus	80	75.0	.	12.5	*

Table 3 Multivariable models: Effects of environmental parameters (predictor variables) on the number of all (a), threatened (b) and oligolectic bee species (c) within quarries ($N = 16$). Effects were analysed using Generalized Linear Mixed-effects Models (GLMM) (Poisson error structure) with 'subarea' as a random intercept. Model-averaged coefficients (conditional average) were derived from the top-ranked GLMM ($\Delta AIC_C < 3$). R^2_m = variance explained by fixed effects, R^2_c = variance explained by both fixed and random effects (Nakagawa et al., 2017). RI = relative parameter importance (see Section 2.5.2). Statistical significance is indicated as follows: n.s. = not significant; $P \geq 0.05$; *$P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Parameter	**Estimate**	**SE**	**z**	**RI**	***P***
(a) All species ($R^2_m = 0.83–0.90$, $R^2_c = 0.89–0.92$)					
(Intercept)	2.78	0.23	11.00	.	***
Earthen banks/scarps	4.41×10^{-3}	1.02×10^{-3}	3.89	1.00	***
Pollen sources	1.57×10^{-2}	3.92×10^{-3}	3.74	1.00	***
Unvegetated	5.55×10^{-3}	2.17×10^{-3}	2.29	0.40	*
Fringe	5.88×10^{-2}	3.29×10^{-2}	1.54	0.20	n.s.
Habitat heterogeneity (Shannon index)	0.34	0.17	1.73	0.13	n.s.
(b) Threatened species ($R^2_{m/c} = 0.72–0.76$)					
(Intercept)	0.22	0.48	0.42	.	n.s.
Pollen sources	3.18×10^{-2}	8.19×10^{-3}	3.51	1.00	***
Earthen banks/scarps	4.71×10^{-3}	1.90×10^{-3}	2.23	0.77	*
(c) Oligolectic species ($R^2_{m/c} = 0.64–0.67$)					
(Intercept)	0.77	0.41	1.68	.	n.s.
Pollen sources	2.68×10^{-2}	7.16×10^{-3}	3.39	1.00	***
Earthen banks/scarps	2.90×10^{-3}	1.89×10^{-3}	1.38	0.34	n.s.

Within abandoned quarries, species richness of bees (all, threatened and oligolectic species) decreased with the variable 'years since last mining' (Fig. 5). The variable was negatively correlated with the number of pollen sources and cover of annual ruderal vegetation (Table B4, Appendix B). Model accuracy of the GLMMs was high again ($R^2_m = 0.77–0.93$; $R^2_c = 0.87–0.93$).

4. Discussion

Human disturbance through intensive land use is considered the main driver of current insect declines, including bees (Buckles and Harmon-Threatt, 2019; Cardoso et al., 2020; Winfree et al., 2009). However, anthropogenic disturbance such as quarrying is also known to create new habitats for species-rich bee assemblages (Heneberg et al., 2013; Krauss et al., 2009; Twerd et al., 2019). In our study, limestone quarries—in particular active ones—were hotspots of bee diversity. The 159 detected species in the 16 quarries represent 57% of the bee fauna in the entire study area (Esser et al., 2010). The predictors of species richness—pollen sources and nesting habitats—were widely available in both types of quarries and therefore very likely explained the generally high value of quarries for species-rich bee assemblages. Previous studies underline that the diversity of pollen sources (Holzschuh et al., 2008; Roulston and Goodell, 2011; Twerd and Banaszak-Cibicka, 2019) and sufficient nesting sites (Potts et al., 2005; Westrich, 2018) determine habitat quality for bees.

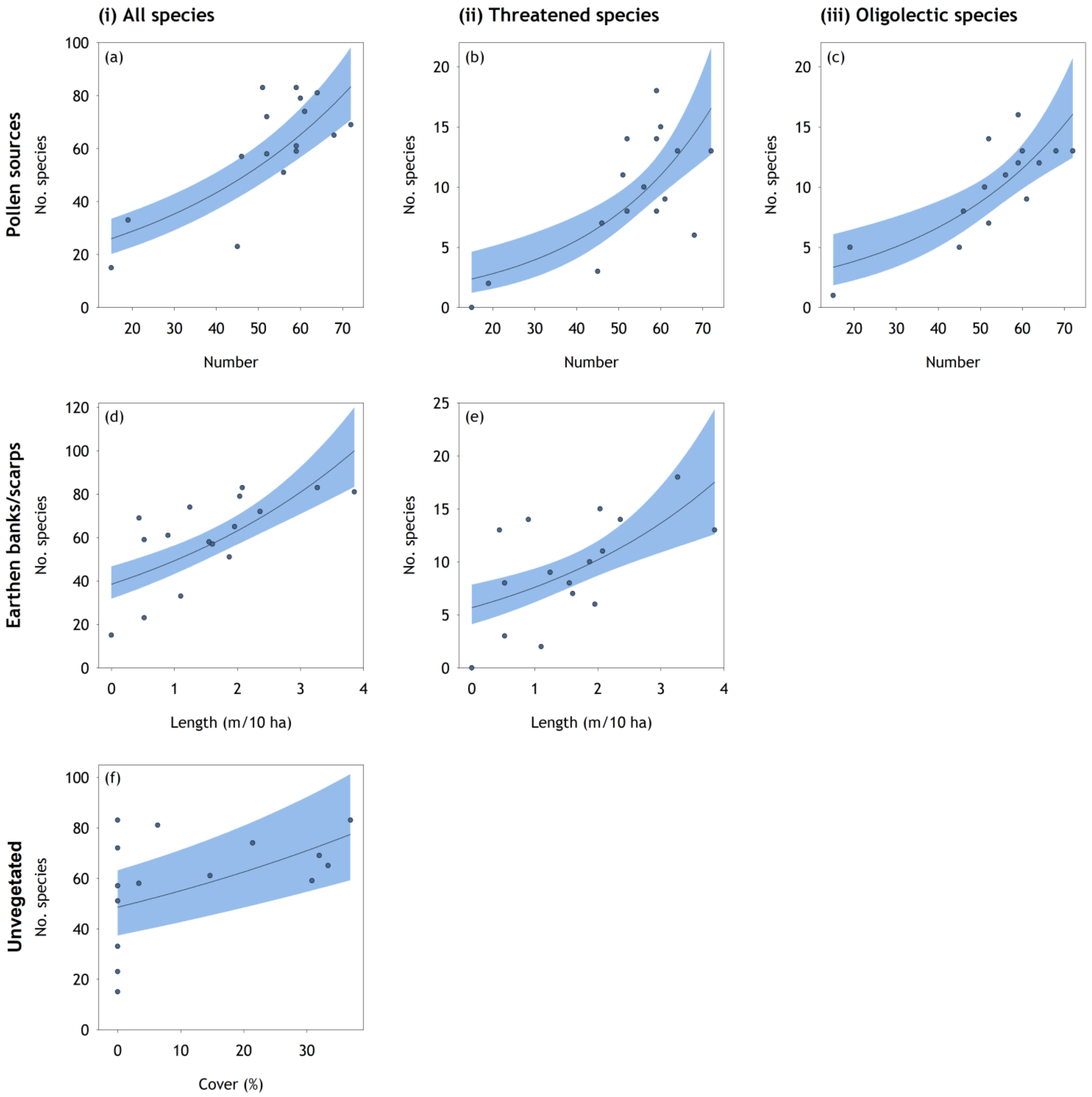

Figure 4 Relationship between several environmental parameters: Pollen sources and the number of all (a), threatened (b) and oligolectic bee species (c), density of earthen banks/scarps and number of all (d) and threatened bee species (e), unvegetated and all bee species (f) within all investigated limestone quarries ($N = 16$) (Table 3). The regression slopes were fitted using univariable Generalized Linear Mixed-effects Models with 'subarea' as a random intercept (for details see Section 2.5). (a) $y = 0.02044 + 2.952362 \times$ (pollen sources), $P < 0.001$, $R^2_m = 0.77$, $R^2_c = 0.87$; (b) $y = 0.03403 + 0.356758 \times$ (pollen sources), $P < 0.001$, $R^2_m = 0.72$, $R^2_c = 0.82$; (c) $y = 0.02751 + 0.796513 \times$ (pollen sources), $P < 0.001$, $R^2_m = 0.64$, $R^2_c = 0.64$; (d) $y = 0.24775 + 3.65082 \times$ (earthen banks/scarps), $P < 0.001$, $R^2_m = 0.74$, $R^2_c = 0.81$; (e) $y = 0.29296 + 1.73599 \times$ (earthen banks/scarps), $P < 0.001$, $R^2_m = 0.45$, $R^2_c = 0.45$; (f) $y = 0.01265 + 3.88289 \times$ (unvegetated), $P < 0.001$, $R^2_m = 0.41$, $R^2_c = 0.87$. Blue hatchings indicate 95% confidence intervals.

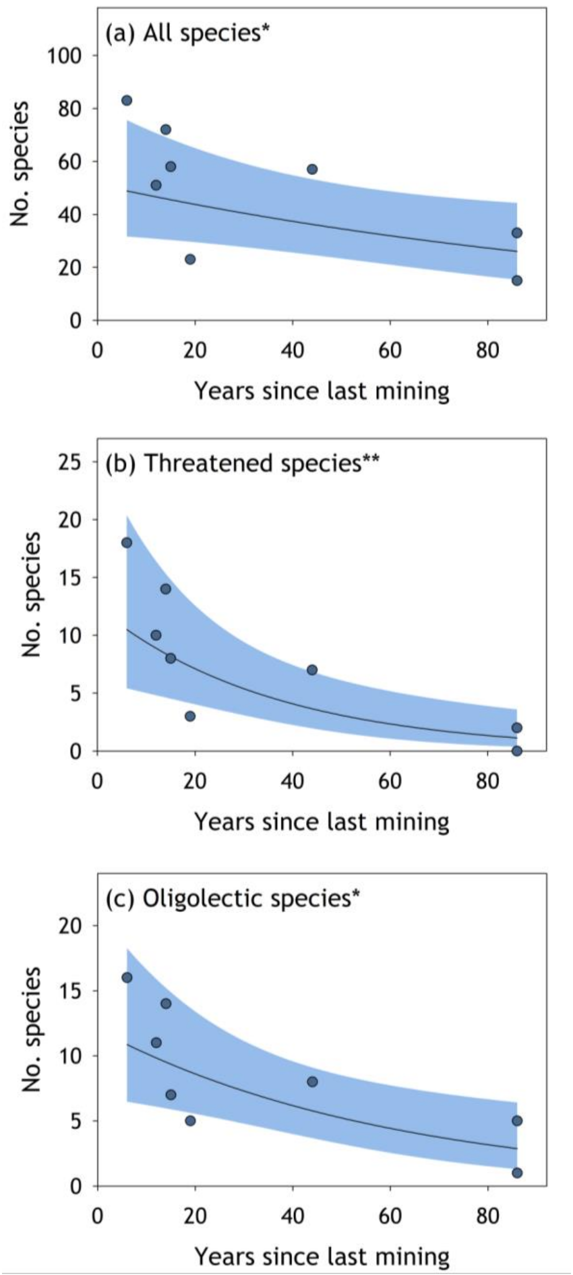

Figure 5 Relationship between the parameter 'years since last mining activitiy' and all (a), threatened (b) and oligolectic (c) bee species within abandoned limestone quarries ($N = 8$). The regression slopes were fitted using univariable Generalized Linear Mixed-effects Models with 'subarea' as a random intercept (for details see Section 2.5). (a) y = 3.936564 – 0.007875 × (years since last mining), $P < 0.05$, $R^2_m = 0.31$, $R^2_c = 0.89$; (b) y = 2.517935 – 0.027782 × (years since last mining), $P < 0.001$, $R^2_m = 0.74$, $R^2_c = 0.85$; (c) y = 2.485633 – 0.016627 × (years since last mining), $P < 0.05$, $R^2_m = 0.61$, $R^2_c = 0.70$. Blue hatchings indicate 95% confidence intervals.

However, habitat quality and composition of bee assemblages differed between the two types of quarries and also changed in abandoned quarries over a time period of 86 years. Although habitat heterogeneity (Shannon index) did not differ between active and abandoned quarries, each type of quarry was characterized by different successional stages. Active quarries were dominated by early-successional stages (unvegetated areas and ruderal vegetation) and had more pollen sources. By contrast, abandoned quarries were composed of later successional stages (shrubby calcareous grasslands, shrubberies and forest). The number of pollen sources fostered species richness of all three considered groups of bees (all, threatened and oligolectic species). It was negatively correlated with annual ruderal vegetation and calcareous grasslands with shrubs. The prior is characteristic of the earliest successional stages of quarry succession while the latter often requires several decades to establish within quarries (Gilcher and Tränkle, 2005; Prach et al., 2011, 2014). In line with this, the availability of pollen sources declined with the variable 'years since last mining' in abandoned quarries.

Generally, nesting sites of bees have to be sunlit, and nearly 60% of the German species depend on bare ground for breeding (Westrich, 2018). As a result, the number of bee species increased with the density of open earthen banks/scarps (all and threatened species) and cover of unvegetated area (all species). The cover of unvegetated area was higher in active compared to abandoned quarries. By contrast, the density of open earthen banks/scarps did not differ between active and abandoned quarries. Nevertheless, we assume that abandoned quarries offered fewer earthen banks/scarps suitable for breeding since many of these microhabitats suffered from shading through taller, later successional vegetation dominated by woody plants. Moreover, as the correlation analysis showed, in the long run, open earthen banks/scarps disappear in abandoned quarries due to ongoing succession.

Patch size is another important driver of species richness in fragmented landscapes (Poniatowski et al., 2018). In our study, all quarries had a size of at least 15 ha and active quarries were larger than abandoned ones. The rationale behind the latter is that nowadays, the approval authorities rather permit the expansion of a mining area directly adjacent to an existing quarry than to establish new quarries in the landscape (pers. comm. H. Escher, Geo park Terra.vita, cf. also Beneš et al., 2003). In our study, the genuine effect of quarry size on species richness of bees was at most weak. Quarry size was correlated with the cover of unvegetated area, which fostered overall species richness of bees (see above). Vertebrates (Suter, 2017) or classical metapopulation species such as butterflies (Salz and Fartmann, 2009) are known to have high area requirements to build viable populations. By contrast, bees do not exploit food resources distant from their nesting habitats and maximum distances between both are 150–600 m (Gathmann and Tscharntke, 2002). Hence, we explain the low importance of quarry size for species richness of bees by the generally large size of the studied quarries and the small home range of bees.

To sum up, limestone quarries were hotspots of bee diversity. However, habitat quality and composition of bee assemblages was strongly dependent on quarry management. Active mining continuously created early-successional stages rich in pollen sources and sunlit nesting habitats, favouring species richness of bees in general and those of threatened and oligolectic species in particular. Successional speed is generally low in quarries (Gilcher and Tränkle, 2005; Münsch and Fartmann, 2022; Prach et al., 2011, 2014). Nevertheless, in abandoned quarries, later successional stages increasingly dominated due to ongoing succession and, hence, habitat quality and species richness of bees decreased.

5. Implications for conservation

Our study highlighted the crucial importance of active quarry management for species-rich bee assemblages. In active quarries, areas with sunlit early-successional stages with a high amount of pollen sources and microhabitats for nesting continuously emerge. Quarries rich in early-successional stages may favour species richness not only of bees but also of other groups of conservation concern such as plants (Gilcher and Tränkle, 2005; Prach et al., 2011, 2014), spiders (Tropek et al., 2010; Tropek and Konvička, 2008), butterflies (Beneš et al., 2003; Münsch and Fartmann, 2022) or birds (Šálek, 2012).

By contrast, despite the low successional speed, abandoned quarries are characterized in the long run by successional shifts from early to later successional stages with adverse effects on species richness of bees and biodiversity in general (Beneš et al., 2003; Münsch and Fartmann, 2022). Accordingly, shrubs and trees have to be removed regularly (Poschlod et al., 1997). Additionally, in quarries in which thick soil layers have already developed, topsoil removal is recommended (Münsch and Fartmann, 2021). Technical reclamation, including backfilling or afforestation, should generally be prohibited since it counteracts current goals of biodiversity conservation (Tropek et al., 2010; Münsch and Fartmann, 2022).

During the last century, central European landscapes have strongly suffered from landscape homogenization and loss of biodiversity (Poschlod et al., 2017; Fartmann et al., 2021). However, particularly in older quarries, species of former traditional landscapes have remained while vanishing from the surrounding landscape (Beneš et al., 2003; Gilcher and Tränkle, 2005; Novak and Konvička, 2006). Present policy favours the enlargement of existing quarries over the establishment of new quarries in the landscape. From a biodiversity conservation perspective, this approach should also be the first choice. Our recommendation is based on three reasons: (i) existing quarries are often already refuges for colonies of rare species that can serve as source populations (Münsch and Fartmann, 2022), (ii) many species of conservation concern are such due to their low mobility and inability to colonize remote habitats (see Section 4) and (iii) in the impoverished modern-day landscapes, source population that may colonize new quarries are often lacking (Gilcher and Tränkle, 2005; Novak and Konvička, 2006).

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Appendix A

List of identification literature

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Appendix B

Table B1 Overview of environmental parameters used for Generalized Linear Mixed-effects Models (GLMM) and their intercorrelations with other environmental parameters (Pearson correlation [*r*], $|r| > 0.6$). $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Parameter	**Surrogate for** (Pearson correlation [*r*])
Macroclimate	
Mean annual temperature (°C)	Elevation (−0.84***); latitude (−0.60*)
Mean annual precipitation (mm)	.
Landscape quality[1]	
Forest	Arable land (−0.73***)
Grassland	.
Urban area	.
Habitat quality	
Habitat types (%)	
Unvegetated	Shrubbery (−0.69*); quarry size (0.69**)
Perennial ruderal vegetation	.
Mesic grassland	.
Calcareous grassland	.
Fringe	.
Forest	.
Habitat heterogeneity (Shannon index)	.
Density earthen bank/scarps (m/10 ha)	.
No. pollen sources	Shrubby calcareous grassland (−0.65**); annual ruderal veg. (0.64**)

[1] Cover of land-use types (%) within a radius of 200 m around each quarry.

Table B2 Univariable models: Influence of environmental parameters (predictor variables) on the number of all, threatened and oligolectic bee species within the quarries (*N* = 16), analysed with Generalized Linear Mixed-effects Models (GLMM) (Poisson error structure). n.s. = not significant; **P* < 0.05; ** *P* < 0.01; *** *P* < 0.001.

Parameter	**All species**			**Threatened species**			**Oligolectic species**		
	Estimate	**SE**	***P***	**Estimate**	**SE**	***P***	**Estimate**	**SE**	***P***
Macroclimate									
Mean annual temperature (°C)	-1.89×10^{-1}	1.37×10^{-1}	n.s.	-2.44×10^{-1}	2.06×10^{-1}	n.s.	-2.62×10^{-1}	1.99×10^{-1}	n.s.
Mean annual precipitation (mm)	-1.10×10^{-3}	5.15×10^{-4}	n.s.	-1.54×10^{-3}	1.16×10^{-3}	n.s.	-9.97×10^{-2}	9.98×10^{-1}	n.s.
Landscape quality[1]									
Forest	1.28×10^{-3}	1.97×10^{-3}	n.s.	1.54×10^{-3}	3.67×10^{-3}	n.s.	3.62×10^{-3}	3.54×10^{-3}	n.s.
Grassland	-1.83×10^{-3}	2.30×10^{-3}	n.s.	1.48×10^{-3}	4.58×10^{-3}	n.s.	-1.62×10^{-3}	5.90×10^{-3}	n.s.
Urban area	4.06×10^{-3}	3.38×10^{-3}	n.s.	5.70×10^{-3}	1.09×10^{-2}	n.s.	4.19×10^{-3}	8.26×10^{-3}	n.s.
Habitat quality									
Habitat types (%)									
Vegetation–free area	1.26×10^{-2}	1.95×10^{-3}	***	1.08×10^{-2}	5.03×10^{-3}	*	1.13×10^{-2}	4.82×10^{-3}	*
Perennial ruderal vegetation	2.21×10^{-2}	5.51×10^{-3}	***	2.06×10^{-2}	1.37×10^{-2}	n.s.	2.81×10^{-2}	1.30×10^{-2}	*
Mesic grassland	-2.13×10^{-2}	1.48×10^{-2}	n.s.	-2.79×10^{-2}	3.00×10^{-2}	n.s.	-3.24×10^{-2}	2.98×10^{-2}	n.s.
Calcareous grassland	-1.26×10^{-2}	4.10×10^{-3}	**	-1.88×10^{-2}	1.14×10^{-2}	n.s.	-9.47×10^{-3}	9.60×10^{-3}	n.s.
Fringe	1.25×10^{-1}	2.72×10^{-2}	***	9.33×10^{-2}	4.71×10^{-2}	*	8.24×10^{-2}	4.58×10^{-2}	n.s.
Forest	-1.60×10^{-2}	2.64×10^{-3}	***	-2.57×10^{-2}	7.46×10^{-3}	***	-2.09×10^{-2}	6.78×10^{-3}	***
Habitat heterogeneity	3.61×10^{-1}	1.51×10^{-1}	*	3.02×10^{-1}	3.71×10^{-1}	n.s.	2.22×10^{-1}	3.71×10^{-1}	n.s.
Earthen banks/scarps (m/10 ha)	6.12×10^{-3}	1.01×10^{-3}	***	7.24×10^{-3}	1.87×10^{-3}	***	5.18×10^{-3}	1.84×10^{-3}	**
No. Pollen sources	2.04×10^{-2}	2.66×10^{-3}	***	3.40×10^{-2}	7.67×10^{-3}	***	2.75×10^{-2}	6.97×10^{-3}	***

[1] Cover of land-use types (%) within a radius of 200 m around each quarry.

Table B3 Frequencies (%) of all observed bee species in active ($N = 8$) and abandoned limestone quarries ($N = 8$). Pollen specificity: oligolectic (oligo) according to Westrich (2018); Threat status (TS): x = threatened species according to Esser et al. (2010).

Species	**Quarry type**		**Pollen specificity**	**TS**
	Active	**Abandoned**		
Andrena barbilabris	12.5	0.0	.	.
Andrena batava	0.0	25.0	oligo	x
Andrena bicolor	75.0	87.5	.	.
Andrena carantonica	50.0	0.0	.	.
Andrena chrysosceles	62.5	50.0	.	.
Andrena cineraria	87.5	62.5	.	.
Andrena clarkella	50.0	87.5	oligo	.
Andrena dorsata	25.0	0.0	.	.
Andrena flavipes	100.0	62.5	.	.
Andrena fucata	12.5	12.5	.	.
Andrena fulva	50.0	37.5	.	.
Andrena gravida	100.0	25.0	.	.
Andrena haemorrhoa	100.0	50.0	.	.
Andrena helvola	12.5	0.0	.	.
Andrena humilis	0.0	12.5	oligo	x
Andrena labiata	25.0	0.0	.	.
Andrena minutula	75.0	75.0	.	.
Andrena minutuloides	50.0	0.0	.	.
Andrena nigroaenea	100.0	87.5	.	.
Andrena nitida	75.0	62.5	.	.
Andrena nycthemera	0.0	12.5	oligo	x
Andrena ovatula	37.5	25.0	.	.
Andrena praecox	100.0	87.5	oligo	.
Andrena proxima	37.5	0.0	oligo	.
Andrena ruficrus	0.0	25.0	oligo	x
Andrena strohmella	87.5	37.5	.	.
Andrena subopaca	62.5	50.0	.	.
Andrena vaga	37.5	12.5	oligo	.
Andrena varians	0.0	12.5	.	.
Andrena viridescens	12.5	12.5	oligo	.
Andrena wilkella	37.5	25.0	oligo	.
Anthidium byssinum	0.0	12.5	oligo	x
Anthidium manicatum	62.5	12.5	.	.
Anthidium oblongatum	12.5	0.0	.	x
Anthidium punctatum	87.5	75.0	.	x
Anthidium strigatum	75.0	75.0	.	.
Anthophora aestivalis	87.5	50.0	.	x
Anthophora plumipes	75.0	75.0	.	.
Bombus bohemicus	87.5	75.0	.	.
Bombus campestris	12.5	0.0	.	x
Bombus hortorum	75.0	62.5	.	.

Table B3 Continued.

Species	Quarry type		Pollen specificity	TS
	Active	Abandoned		
Bombus hypnorum	37.5	37.5	.	.
Bombus lapidarius	100.0	100.0	.	.
Bombus lucorum	50.0	50.0	.	.
Bombus pascuorum	100.0	100.0	.	.
Bombus pratorum	50.0	37.5	.	.
Bombus rupestris	50.0	0.0	.	.
Bombus sylvarum	25.0	0.0	.	x
Bombus sylvestris	50.0	50.0	.	.
Bombus terrestris	100.0	100.0	.	.
Bombus vestalis	37.5	0.0	.	.
Ceratina cyanea	75.0	50.0	.	.
Chelostoma campanularum	37.5	37.5	oligo	.
Chelostoma florisomne	12.5	0.0	oligo	.
Chelostoma rapunculi	12.5	25.0	oligo	.
Coelioxys afra	25.0	0.0	.	.
Coelioxys aurolimbata	12.5	0.0	.	x
Coelioxys mandibularis	50.0	25.0	.	.
Coelioxys rufescens	12.5	0.0	.	x
Colletes cunicularius	100.0	62.5	oligo	.
Colletes daviesanus	75.0	25.0	oligo	.
Colletes fodiens	12.5	0.0	oligo	x
Colletes similis	87.5	37.5	oligo	x
Colletes succinctus	0.0	12.5	oligo	x
Dasypoda hirtipes	12.5	12.5	oligo	x
Epeolus variegatus	50.0	37.5	.	.
Eucera longicornis	0.0	12.5	oligo	x
Halictus quadricinctus	25.0	0.0	.	x
Halictus rubicundus	12.5	37.5	.	.
Halictus scabiosae	75.0	37.5	.	.
Halictus simplex	12.5	12.5	.	.
Halictus tumulorum	50.0	75.0	.	.
Heriades truncorum	62.5	50.0	oligo	.
Hylaeus annularis	62.5	50.0	.	x
Hylaeus brevicornis	50.0	25.0	.	.
Hylaeus communis	75.0	50.0	.	.
Hylaeus confusus	37.5	50.0	.	.
Hylaeus cornutus	25.0	25.0	.	.
Hylaeus difformis	12.5	0.0	.	.
Hylaeus gibbus	0.0	12.5	.	.
Hylaeus gredleri	87.5	12.5	.	.
Hylaeus hyalinatus	37.5	37.5	.	.
Hylaeus moricei	25.0	0.0	.	.
Hylaeus nigritus	62.5	37.5	oligo	x

Table B3 Continued.

Species	Quarry type		Pollen specificity	TS
	Active	Abandoned		
Hylaeus paulus	62.5	37.5	.	.
Hylaeus signatus	100.0	37.5	oligo	.
Lasioglossum albipes	0.0	12.5	.	.
Lasioglossum brevicorne	12.5	0.0	.	x
Lasioglossum calceatum	100	37.5	.	.
Lasioglossum costulatum	12.5	0.0	oligo	x
Lasioglossum fulvicorne	0.0	12.5	.	.
Lasioglossum laevigatum	0.0	12.5	.	x
Lasioglossum laticeps	87.5	62.5	.	.
Lasioglossum lativentre	12.5	12.5	.	x
Lasioglossum leucopus	0.0	12.5	.	.
Lasioglossum leucozonium	50.0	50.0	.	.
Lasioglossum malachurum	12.5	0.0	.	x
Lasioglossum minutissimum	12.5	0.0	.	.
Lasioglossum minutulum	12.5	0.0	.	x
Lasioglossum morio	100	87.5	.	.
Lasioglossum nitidiusculum	50.0	12.5	.	x
Lasioglossum nitidulum	25.0	25.0	.	x
Lasioglossum parvulum	37.5	37.5	.	x
Lasioglossum pauxillum	100.0	87.5	.	.
Lasioglossum quadrinotatum	12.5	0.0	.	x
Lasioglossum semilucens	0.0	12.5	.	.
Lasioglossum villosulum	75.0	87.5	.	.
Lasioglossum xanthopus	12.5	0.0	.	x
Macropis fulvipes	12.5	0.0	oligo	x
Megachile alpicola	0.0	12.5	.	x
Megachile centuncularis	50.0	0.0	.	.
Megachile circumcincta	25.0	0.0	.	x
Megachile ericetorum	62.5	25	oligo	.
Megachile nigriventris	12.5	0.0	.	.
Megachile pillidens	50.0	0.0	.	.
Megachile versicolor	75.0	75.0	.	.
Megachile willughbiella	75.0	25.0	.	.
Melecta albifrons	62.5	12.5	.	.
Melitta haemorrhoidalis	12.5	37.5	oligo	.
Nomada alboguttata	25.0	25.0	.	x
Nomada bifasciata	75.0	25.0	.	.
Nomada conjungens	62.5	12.5	.	.
Nomada fabriciana	75.0	62.5	.	.
Nomada ferruginata	0.0	25.0	.	x
Nomada flava	75.0	50.0	.	.
Nomada flavoguttata	100.0	100.0	.	.
Nomada fucata	75.0	37.5	.	.

Table B3 Continued.

Species	**Quarry type**		**Pollen specificity**	**TS**
	Active	**Abandoned**		
Nomada goodeniana	62.5	25.0	.	.
Nomada lathburiana	25.0	12.5	.	.
Nomada leucopthalma	25.0	12.5	.	.
Nomada marshamella	87.5	62.5	.	.
Nomada succincta	75.0	50.0	.	.
Osmia adunca	75.0	12.5	oligo	x
Osmia anthocopoides	25.0	12.5	oligo	x
Osmia aurulenta	62.5	62.5	.	x
Osmia bicolor	62.5	62.5	.	x
Osmia bicornis	87.5	50.0	.	.
Osmia leucomelana	75.0	50.0	.	.
Osmia parietina	0.0	12.5	oligo	x
Osmia spinulosa	75.0	62.5	oligo	x
Osmia tridentata	25.0	12.5	oligo	x
Osmia uncinata	0.0	12.5	.	.
Panurgus banksianus	12.5	0.0	oligo	x
Panurgus calcaratus	12.5	12.5	oligo	.
Sphecodes albilabris	75.0	62.5	.	.
Sphecodes crassus	75.0	25.0	.	.
Sphecodes ephippius	87.5	75.0	.	.
Sphecodes ferruginatus	12.5	25.0	.	.
Sphecodes geofrellus	75.0	12.5	.	.
Sphecodes gibbus	25.0	25.0	.	.
Sphecodes miniatus	50.0	25.0	.	.
Sphecodes monilicornis	75.0	62.5	.	.
Sphecodes niger	12.5	0.0	.	.
Sphecodes pellucidus	12.5	0.0	.	.
Sphecodes puncticeps	12.5	0.0	.	.
Stelis breviuscula	12.5	0.0	.	.
Stelis ornatula	0.0	12.5	.	.

Table B4 Overview of the habitat-quality parameters that significantly correlated with the predictor 'years since last mining' for abandoned quarries (*n* = 8). Pearson correlation [*r*], |*r*| > 0.6. **P* < 0.05; ***P* < 0.01; ****P* < 0.001.

Parameter	**Years since last mining**
Annual ruderal vegetation (%)	−0.92***
Perennial ruderal vegetation (%)	−0.83**
Density of earthen banks/scarps (m)	−0.84**
Quarry size (ha)	−0.75*
No. pollen sources	−0.97***

Kettermann & Fartmann (in Überarbeitung): *Ecological Engineering*

Quarry ponds are hotspots of amphibian species richness and newt abundance

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Abstract

Amphibians are among the most severely declining taxonomic group worldwide. Recent studies have shown that quarries may have a high conservation value for biodiversity conservation. However, well-replicated research on the importance of quarry ponds for amphibian assemblages has been scarce thus far. The aim of this study was to compare the environmental conditions and composition of amphibian assemblages of 15 randomly selected quarry ponds with those of 15 control ponds in the surrounding landscape. For each pond, we assessed several parameters of habitat and landscape quality. The effects of environmental conditions on overall species richness, number of threatened species and newt abundance were analysed using Generalised Linear Mixed-effects Models. Our study revealed strong differences in habitat quality and composition of amphibian assemblages between quarry and control ponds. In particular, a larger area of the semi-aquatic zone, a longer sunshine duration, more bare soil at the shoreline and the absence of fish were typical of quarry ponds, whereas a taller vegetation at the shoreline characterized control ponds. As a result, overall species richness, number of threatened species and newt abundance were higher in quarry ponds compared with control ponds. Overall, quarry ponds had a higher habitat quality than control ponds. In particular, (i) the large area of sunlit and warm microhabitats and (ii) the absence of fish predators favoured species richness of amphibians and newt abundance at the quarry ponds. Consequently, quarry ponds—thanks to their early-successional stages—have a high conservation value for amphibians.

Keyword: Biodiversity conservation; early-successional stage; global change; habitat quality; mining site; warm microclimate

1. Introduction

Biodiversity loss is accelerating continuously and, therefore, is one of the most critical global issues of our time (Rockström et al., 2009; Butchart et al., 2010; Naeem et al., 2012). The worldwide speed of extinction is currently 1,000 times higher than the natural background rate (Pimm et al., 2014; De Vos et al., 2015). In terrestrial biomes, land-use change is seen as the main driver of the recent biodiversity crisis (Newbold et al., 2015; Cardoso et al., 2020). In particular, intensification and abandonment of traditional land use have led to a dramatic loss of natural and semi-natural habitats. As a result, the remaining habitat fragments and their biodiversity are often highly isolated and suffer from the deterioration of habitat quality (Arntzen et al., 2017; Poniatowski et al., 2018; Münsch et al., 2019).

For a long time, quarries had a bad image among conservationists and were associated with negative effects on biodiversity (Beneš et al., 2003; Tropek et al., 2010). Indeed, quarrying results in fundamental changes of the environmental conditions, since existing vegetation and top soil are removed (Bétard, 2013; Kalarus et al., 2019). However, it also creates vast areas of early-successional stages. Such seral stages are among the most rapidly declining habitats in our landscapes and often harbour assemblages rich in thermophilic and threatened species (Poschlod and Braun-Reichert, 2017; Fartmann et al., 2021). So far, recent studies have shown that quarries may have a high conservation value for birds (Šálek, 2012; Salgueiro et al., 2020), arthropods (Beneš et al., 2003; Tropek et al., 2008; Tropek et al., 2010; Münsch et al., 2022; Kettermann et al., 2022) and vascular plants (Tropek et al., 2010; Řehounková et al., 2020). By contrast, well-replicated research on quarry ponds and their species assemblages is still lacking.

Amphibians are among the most severely declining taxonomic groups worldwide (Stuart et al., 2004; Wake and Vredenburg, 2008; Cordier et al., 2021). It is assumed that approximately 50% of the global amphibian species are threatened by extinction (González-del-Pliego et al., 2019). One of the main drivers of this dramatic decline is habitat loss (Cushman, 2006; Hof et al., 2011; Arntzen et al., 2017; Murray et al., 2020; Cordier et al., 2021). Additionally, amphibians suffer from climate change (Hof et al., 2011; Murray et al., 2020), introduced alien species (Kats and Ferrer, 2003) and infectious diseases (Yap et al., 2017; DiRenzo and Grant, 2019). Amphibians are dependent on a high habitat quality of the water bodies used for breeding. In particular, sunlit and warm water bodies with low predator densities, such as fish, are of crucial importance for successful reproduction (cf. Hartel et al., 2007; Shulse et al., 2012; Drayer and Richter, 2016; Rannap et al., 2020; Cox et al., 2017). Since amphibians have a bipartite life cycle with aquatic and terrestrial stages (Stuart et al., 2004; Cushman, 2006), landscape quality also plays a significant role (Cox et al., 2017; Holtmann et al., 2017).

The aim of this study was to compare the environmental conditions and composition of amphibian assemblages of 15 randomly selected quarry ponds with those of 15 control ponds in the surrounding landscape. For each pond, we assessed several parameters of habitat and landscape quality. The effects of environmental conditions on overall species richness, number of threatened species and newt abundance were analysed using Generalised Linear Mixed-effects Models. Finally, based on the results of this study, we developed management recommendations for quarry ponds to enhance amphibian species richness and abundance.

2. Material and methods

2.1. Study area

The study area was located in the eastern part of the German Federal State of North Rhine-Westphalia (Central Europe) and covered approximately 1,516 km^2. It was divided into three subareas: (i) Beckumer Berge, (ii) Ostwestfalen-Lippe and (iii) Hellweg (Fig. 1). The climate is suboceanic with a mean annual temperature of 9.5 °C and a mean annual precipitation of 951 mm (meteorological station Bad Lippspringe [157 m a.s.l]; period: 1981–2010; DWD, 2021). The subarea Ostwestfalen-Lippe comprises a mosaic of forested hills and ridges as well as flat valleys mainly covered by grassland at an elevation of 250 to 350 m a.s.l. The subareas Beckumer Berge and Hellweg are located in the Westphalian Basin and have an elevation range of 100 to 197 m a.s.l. In both subareas, agriculture is the dominant type of land use. The limestone is mined in quarries and used for the production of gravel, bricks, building material or cement.

2.2. Study plots

In the study area, we randomly selected a total of 15 ponds within limestone quarries (Fig. 1). As a control, the closest pond to the respective quarry pond was chosen in the surrounding landscape.

2.3. Sampling design

During the breeding period of the amphibians from the beginning of March to early May 2019, each pond was visited four times, twice at night and twice during the day. Different methods were used due to the varying phenology and activity patterns of each species (Glandt, 2014). *Rana temporaria* was detected by spawn clumps during the day in early March (Hachtel et al., 2009; Holtmann et al., 2017). Green frogs (*Pelophylax* kl. *esculentus*, *P. lessonae*) were recorded at daytime through visual and acoustic observation in early May. In accordance with Hachtel et al. (2009), the two night surveys were conducted between sunset and midnight. *Bufo bufo* were surveyed using a torch at the end of March and the beginning of April (Hachtel et al., 2009). *Alytes obstetricans*, *Epidalea calamita* and *Hyla arborea* were recorded by calling surveys during warm nights in April. *Salamandra salamandra* was detected during each of the four surveys by turning wood and stones near the shoreline.

Additionally, newt species (*Ichthyosaura alpestris*, *Lissotriton helveticus*, *Lissotriton vulgaris* and *Triturus cristatus*) were caught and counted by using bottle traps (Kronshage et al., 2014). For this purpose, five bottle traps were placed in each pond in early April for one night. For further analyses, we used the number of caught individuals per trap and night as a measure for activity abundance (hereinafter referred to as newt abundance).

Amphibian species were classified in the field according to Glandt (2011) and Tetzlaff (2007). For statistical analysis, we used three response variables: (i) number of all species, (ii) number of threatened species and (iii) newt abundance. Amphibians were considered ‘threatened’ if they were listed as critically endangered, endangered, vulnerable or near threatened in the red data book of North Rhine-Westphalia (LANUV NRW, 2011).

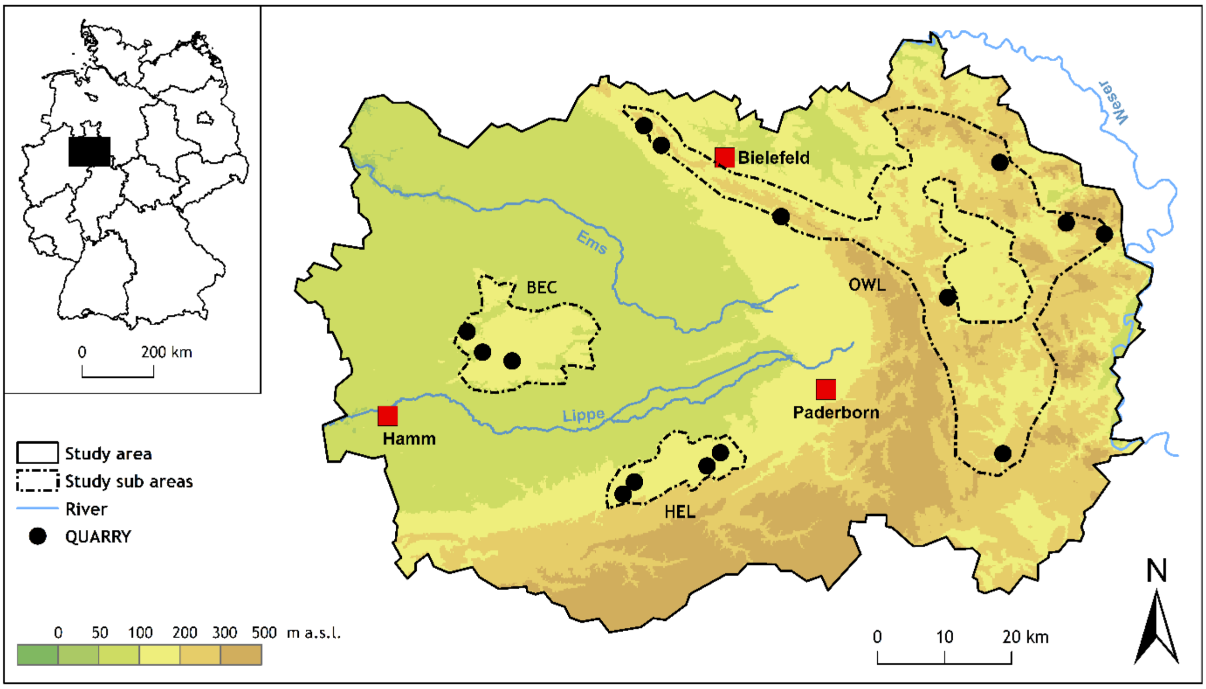

Fig. 1. Location of the study area in the eastern part of North Rhine-Westphalia in central Germany (inlay) and of the three subareas Beckumer Berge (BEC), Ostwestfalen-Lippe (OWL) and Hellweg (HEL) with its plots (limestone quarries).

2.4. *Environmental parameters*

For each studied pond, we sampled several environmental parameters of habitat quality and landscape quality (Table 1). The pH and conductivity were measured during each of the four visits. Prior to statistical analysis, the data were averaged per parameter and pond. Sunshine duration was measured at the first (spring) and the last visit (summer) by using a horizontoscope (Holtmann et al., 2017). Occurrence of fish was sampled by visual inspection during each survey (Table 2). Data on annual temperature (°C) (long-term mean: 1981–2010) were available from 1-km^2 grid datasets of Germany's National Meteorological Service (DWD, 2021) (Table 1). All other field parameters were recorded once between the end of April and early May. For spatial analyses, we used ArcGIS 10.3.1 and aerial photographs. We calculated the distance to the next three water bodies (geometric mean) as a measure of pond connectivity (Eichel and Fartmann, 2008; Poniatowski and Fartmann, 2010; Holtmann et al., 2017).

2.5. *Statistical analysis*

All statistical analyses were performed using R 4.1.2. (R Development Core Team, 2022). Generalised Linear Mixed-effects Models (GLMM) were fitted with 'subarea' (see Section 2.1) as a random intercept (*lme4* package; Bates et al., 2021). To reduce overdispersion within the models, observation-level random effects were added as a random factor (Harrison, 2014, 2015).

Since our study was based on a paired design, all metric environmental parameters (see Section 2.4) and the three response variables (number of all species, number of threatened species and newt abundance; see Section 2.3) were tested for significant differences between quarry and control ponds by using univariable GLMMs. Poisson error structure was applied for count data, while proportional binomial error structure was used for cover data. The corresponding pairs of quarry and control ponds were nested within 'subarea' and used as a random factor in all models. The significance of the predictor variable was assessed with likelihood-ratio tests (Type III tests).

In order to detect environmental parameters that explain species richness of all species and threatened species as well as of newt abundance, we conducted multivariable GLMMs. In a preparatory step, prior to the analyses, we tested all predictor variables for multicollinearity. If two or more variables were intercorrelated (Spearman rank correlation $|r_s| > 0.5$; Table A2), just one—the ecologically comprehensible variable—was used for statistical modelling (Dormann et al., 2013). In a second step, univariable GLMMs were fitted for all combinations of response and predictor variables in order to detect which predictor variables had an impact on the given response variable (Likelihood Ratio Tests, $P < 0.05$) (See Table A1). In the last step, the multivariable models were calculated incorporating all significant variables of the univariable models. In order to identify the most relevant environmental parameters and their relative importance (RI) within our models, we applied model averaging based on an information-theoretic approach (Grueber et al., 2011).

Model averaging was conducted using the 'dredge' function (R package MuMIn; Bartoń, 2021) and only included top-ranked models within $\Delta AIC_C < 3$ (cf. Grueber et al., 2011). We evaluated the explanatory power of the models by calculating marginal (variance explained by fixed effects) and conditional (variance explained by both fixed and random effects) R^2 (Nakagawa et al., 2017).

A Principal Component Analysis (PCA) was conducted to assess the relationship between environmental parameters and pond type (Fig. 5). Differences in nominal variables were tested using Fisher's exact test. Differences in absolute frequencies of each species between the two pond types were analysed with a Chi-squared test.

3. Results

3.1. Environmental parameters

Our study revealed clear differences in habitat quality but not in landscape quality between quarry and control ponds (Table 1). At quarry ponds, the semi-aquatic zone accounted for most of the pond area and overall, it was larger compared with those of control ponds. Additionally, the sunshine duration (spring and summer) was generally higher and, along the shoreline, the cover of trees was lower, the cover of bare soil higher and vegetation shorter at quarry ponds than at control ponds. Occurrence of fish also differed between both types of ponds (Table 2). Quarry ponds were, with one exception, never occupied by fish. By contrast, fish were present in nearly one half of the control ponds. The strong differences in environmental conditions between the two pond types were confirmed by the PCA, which showed a clear separation of control and quarry ponds along the first axis (Fig. 2, Table A3). In particular, a taller vegetation at the shoreline was characteristic of control ponds, whereas a larger area of the semi-aquatic zone, a longer sunshine duration in spring and more bare soil at the shoreline were typical of quarry ponds.

Table 1 Overview of environmental parameters (mean ± SE, minimum and maximum). Differences in parameters between quarry ponds (Quarry, *N* = 15) and control ponds (Control, *N* = 15) were analysed using Generalized Linear Mixed-effects Models (Poisson error structure for count data, proportional binomial error structure for cover data) with 'subarea' as a random intercept (for details see Section 2.5). n.s. = not significant, * *P* <0.05; ** *P* <0.01; *** *P* <0.001.

Parameter	**Quarry**		**Control**		***P***
	Mean (± SE)	Min.–Max.	Mean (± SE)	Min.–Max.	
Habitat quality					
Pond size (m^2)[1]	1,443 ± 394	73–5,811	868 ± 161	106– 1,763	n.s.
pH[2]	7.6 ± 0.1	7.1–8.0	7.4 ± 0.1	7.1–8.0	n.s.
Conductivity (µS/cm)[2]	436 ± 136	261–682	528 ± 52	255–918	n.s.
Sunshine duration spring (h/day)[3]	10.4 ± 0.5	6–12	8.1 ± 0.7	4–13	**
Sunshine duration summer (h/day)[3]	12.8 ± 0.5	9–15	6.8 ± 1.1	2–14	***
Cover semi-aquatic zone (%)	80.0 ± 5.2	30–100	37.6 ± 9.1	10–100	***
Vegetation cover shoreline (%)					
Trees	2.3 ± 0.8	0–10	23.0 ± 6.0	0–65	**
Shrubs	16.8 ± 3.2	2.5–45.0	14.3 ± 4.0	0–40	n.s.
Field layer	16.0 ± 2.6	2.5–35.0	22.3 ± 4.7	5–60	n.s.
Litter	39.3 ± 4.4	5–65	40.0 ± 2.9	20–60	n.s.
Bare soil	30.0 ± 6.9	0–90	3.2 ± 1.1	0–15	***
Vegetation height shoreline (cm)	32.7 ± 3.0	19–58	50.1 ± 5.4	20–102	**
Cover submerged macrophytes (%)	29.3 ± 6.4	0–80	20.7 ± 5.0	0–50	n.s.
Landscape quality					
Elevation (m a.s.l.)[4]	167 ± 13	98–273	147 ± 14	91–259	n.s.
Annual temperature (°C)[5]	9.3 ± 0.1	8.8–9.8	9.4 ± 0.1	8.5–9.9	n.s.
Pond connectivity (m)[6]	789 ± 222	39–2479	481 ± 115	29–1306	n.s.

[1] Calculated from aerial photographs by using ArcGIS 10.3.1.

[2] Measured by using a multi-parameter probe (Hanna HI 98129).

[3] Measured by using a horizontoscope; mean of four measures at N, E, S, W (Holtmann et al., 2017).

[4] Elevation was taken from topographic maps.

[5] Long-term mean (1981–2010) from 1-km^2 grid datasets of Germany's National Meteorological Service (DWD, 2021).

[6] Geometric mean of the distance to the next three water bodies.

Table 2 Absolute and relative frequencies of the categorical variable 'occurrence of fish' at quarry ponds and control ponds. Differences in absolute frequencies between the two groups were analysed with Fisher's exact test. * *P* <0.05.

Parameter	**Quarry**		**Control**		***P***
	N	%	N	%	
Fish					*
Present	1	12.5	7	87.5	
Absent	14	63.6	8	36.4	

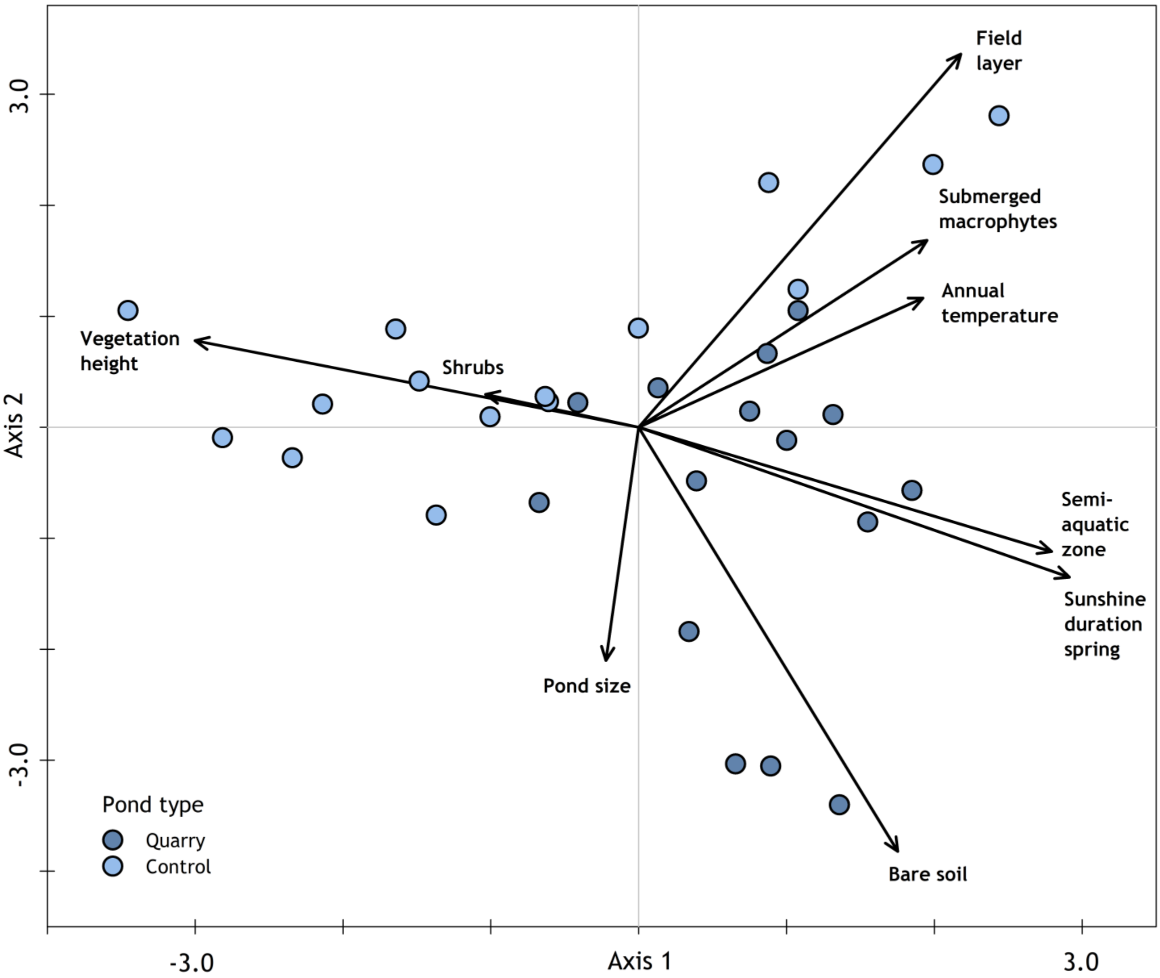

Fig. 2. Principal Component Analysis (PCA): Biplot based on the two pond types and sampled environmental parameters.

3.2. Response of amphibian assemblages to environmental conditions

Altogether, we detected 12 amphibian species, including five threatened species (*Alytes obstetricans*, *Epidalea calamita*, *Hyla arborea*, *Pelophylax lessonae* and *Triturus cristatus*) (Fig. 3). Three species,

A. obstetricans, *Lissotriton vulgaris* and *T. cristatus*, had a higher frequency in quarry ponds compared with control ponds, and there were even three species observed only in quarry ponds (*A. obstetricans*, *E. calamita* and *Salamandra salamandra*). Moreover, overall species richness, number of threatened species and newt abundance were higher in quarry ponds compared with control ponds (Fig. 4).
In the GLMM analyses, assemblage composition was only determined by habitat quality, not landscape quality—more precisely by the area of the semi-aquatic zone and sunshine duration in spring (Table 3, Fig. 5). Overall, species richness and newt abundance increased with the extent of the semi-aquatic zone. By contrast, the number of threatened species was fostered by sunshine duration.

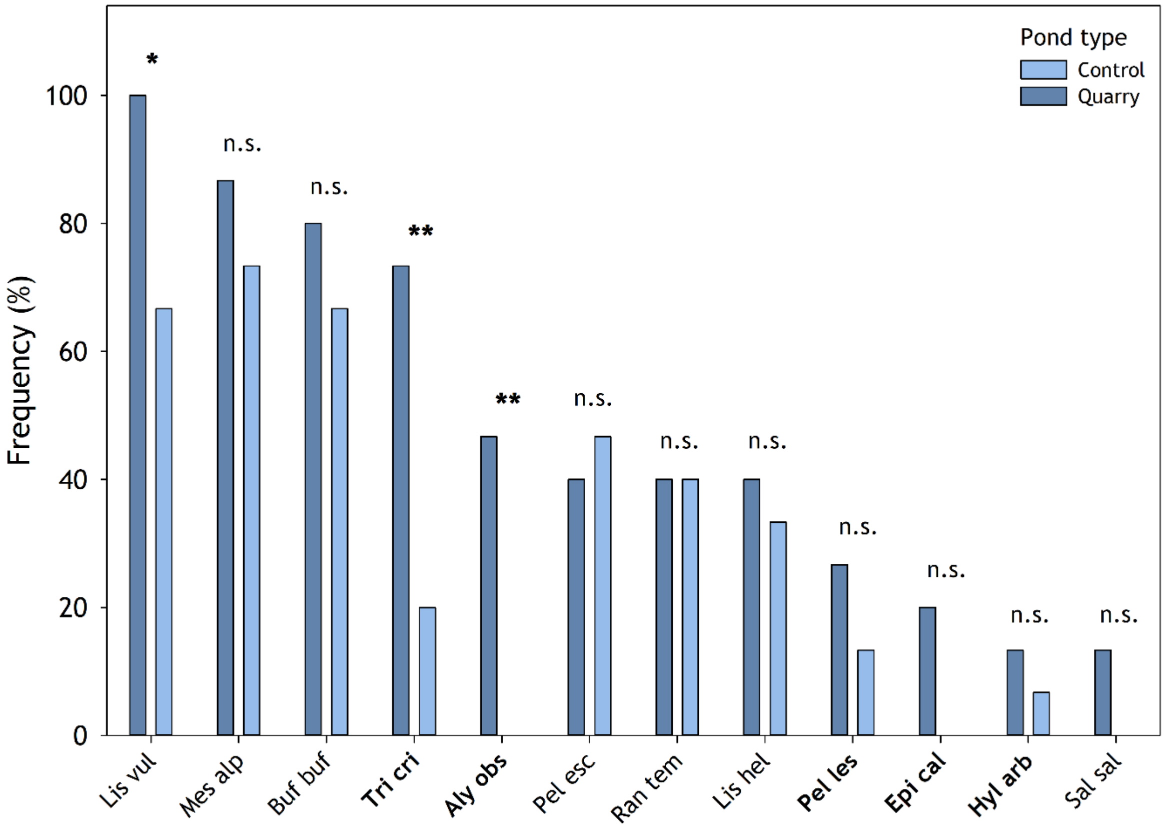

Fig. 3. Frequency of amphibian species in quarry ponds (Quarry, *N* = 15) and control ponds (Control, *N* = 15). Differences in absolute frequencies were tested by Chi-squared test. Abbreviations of species names: Lis vul = *Lissotriton vulgaris*, Mes alp = *Mesotriton alpestris*, Buf buf = *Bufo bufo*, Tri cri = *Triturus cristatus*, Aly obs = *Alytes obstetricans*, Pel esc = *Pelophylax* kl. *esculentus*, Ran tem = *Rana temporaria*, Lis hel = *Lissotriton helveticus*, Pel les = *Pelophylax lessonae*, Epi cal = *Epidalea calamita*, Hyl arb = *Hyla arborea*, Sal sal = *Salamandra salamandra*. Threatened species (LANUV, 2011) are highlighted in bold type. n.s. = not significant; * *P* <0.05; ** *P* <0.01.

4. Discussion

Our study revealed strong differences in habitat quality and composition of amphibian assemblages between quarry and control ponds. In particular, a larger area of the semi-aquatic zone, a longer sunshine duration, more bare soil at the shoreline and the absence of fish was typical of quarry ponds, whereas a taller vegetation at the shoreline characterized control ponds. As a result, overall species richness, number of threatened species and newt abundance were higher in quarry ponds compared with control ponds.

The 12 amphibian species observed in the quarry ponds and generally in this study comprise 80% of the amphibian fauna of the whole study area (cf. Hachtel et al., 2011). Of the three remaining species occurring within the study area, two are extremely rare (*Bombina variegata* and *Pelobates fuscus*) and one has very localized and often allochthonous populations (*Pelophylax ridibundus*). Accordingly, the high completeness of detected species already highlights the high conservation value of quarry ponds for amphibians.

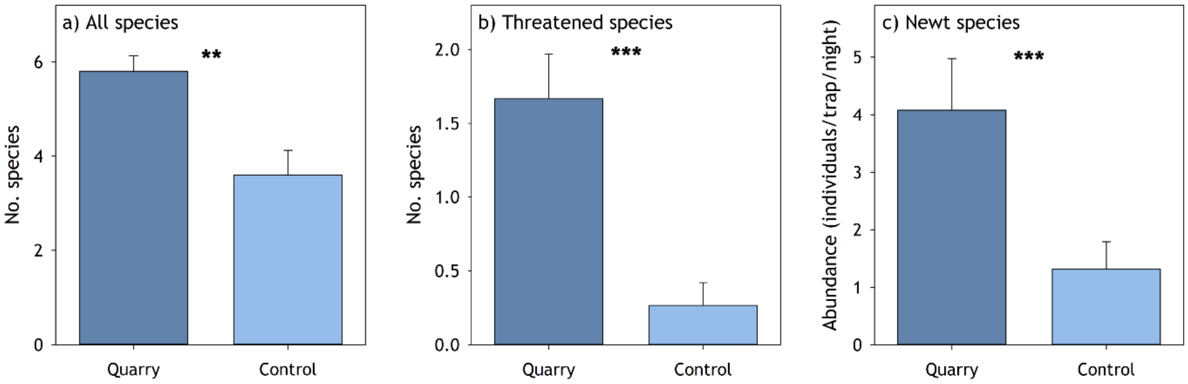

Fig. 4. Mean (± SE) number of all species (a), number of threatened species (b) and newt abundance (c) in quarry ponds (Quarry, $N = 15$) and control ponds (Control, $N = 15$). Differences between pond types were analysed using Generalized Linear Mixed-effects Models (Poisson error structure) with 'subarea' as a random intercept (for details see Section 2.5). ind. = individuals. Statistical significance is indicated as follows: ** $P < 0.01$; *** $P < 0.001$.

The comparison of environmental conditions between the two types of ponds provided further insights into the importance of quarry ponds for amphibians. Quarry ponds exhibited two characteristics that are of crucial importance for species-rich and abundant amphibian assemblages: (i) sunlit and warm microhabitats and (ii) the absence of fish (cf. Hartel et al., 2007; Shulse et al., 2012; Drayer and Richter, 2016; Rannap et al., 2020; Holtmann et al., 2017). A larger area of the semi-aquatic zone and longer sunshine duration (spring and summer) together with a more sparse (lower cover of trees, more bare soil) and shorter vegetation at the shoreline were typical of quarry ponds in comparison with control ponds. Such conditions are known to result in a generally warmer microclimate and higher water temperatures, in particular in the shallow water of the extensive semi-aquatic zone of the quarry ponds (cf. Stoutjesdijk and Barkman, 1992). The majority of the Central European amphibian species (Günther, 2009) and especially those that are thermophilic and threatened, such as *Alytes obstetricans*, *Epidalea calamita*, *Hyla arborea* or *Triturus cristatus* (Richter-Boix et al., 2006; Günther, 2009), depend on warm water bodies for breeding. In line with this, the number of threatened species increased with sunshine duration in spring and a higher cover of the semi-aquatic zone fostered overall species richness and newt abundance. Additionally, the favourable microclimatic conditions were probably at least partly responsible for the higher frequency of *A. obstetricans* and *T. cristatus* as well as the exclusive occurrence of *E. calamita* in quarry ponds.

Table 3 Results of Generalized Linear Mixed-effects Models (GLMM) (Poisson error structure, with 'subarea' as a random intercept): Influence of environmental parameters (predictor variables) on the number of all species (a), on the number of threatened species (b) and newt abundance (c). Model-averaged coefficients (conditional average) were derived from the top-ranked GLMM ($\Delta AIC_C < 3$). R^2_m = variance explained by fixed effects, R^2_c = variance explained by both fixed and random effects (Nakagawa et al., 2017) ($N = 30$). RI = relative parameter importance (see Section 2.5). n.s. = not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Parameter	**Estimate**	**SE**	***Z***	**RI**	***P***
a) No. all species (R^2m = 0.12, R^2c =0.12)					
(Intercept)	1.23	0.18	6.69	.	***
Semi-aquatic zone	5.04×10^{-3}	2.52×10^{-3}	2.00	1.00	*
b) No. threatened species (R^2_m = 0.12–0.30, R^2_c =0.23–0.30)					
(Intercept)	–2.51	1.37	1.77	.	n.s.
Sunshine duration spring	2.36×10^{-1}	1.08×10^{-2}	2.08	0.79	*
Semi-aquatic zone	1.31×10^{-3}	6.94×10^{-3}	1.80	0.66	n.s.
c) Newt abundance (R^2_m = 0.32–0.36, R^2_c =0.98)					
(Intercept)	–0.08	0.70	0.11	.	n.s.
Semi-aquatic zone	2.70×10^{-2}	9.23×10^{-3}	2.77	1.00	**
Bare soil	1.82×10^{-2}	1.42×10^{-2}	1.22	0.29	n.s.

Fish stock has negative effects on amphibian populations due to predation of eggs and larvae and, especially concerning newts, also of adults (Scheffer et al., 2006; Hartel et al., 2007; Rannap et al., 2020). However, in quarry ponds, predation by fish was generally unimportant since fish were only present in one of the ponds. By contrast, fish occurred in almost one half of the control ponds. In general, a large area of the semi-aquatic zone was a surrogate for water bodies free of fish (see Table A3), probably because they had a higher likelihood of drying out in the course of the growing season (own observation) and, hence, hampering the establishment of a permanent fish population. Additionally, in the shallow water of the semi-aquatic zone, eggs, larvae or adults are generally sheltered against predation by larger fish (Caballero-Diaz et al., 2020). Consequently, the positive relationship of the cover of the semi-aquatic zone with overall species richness and newt abundance may not only reflect the importance of warm microclimates but also of microhabitats that are free of fish predators. Therefore, based on the aforementioned, we attribute the higher overall species richness, number of threatened species and newt abundance in quarry ponds to both the favourable microclimatic conditions and the lack of fish predators.

To sum up, quarry ponds had a higher habitat quality than control ponds. In particular, (i) the large area of sunlit and warm microhabitats and (ii) the absence of fish predators favoured species richness of amphibians (overall and threatened species) and newt abundance at the quarry ponds.

Overall, quarry ponds—thanks to their early-successional stages—have a high conservation value for amphibians.

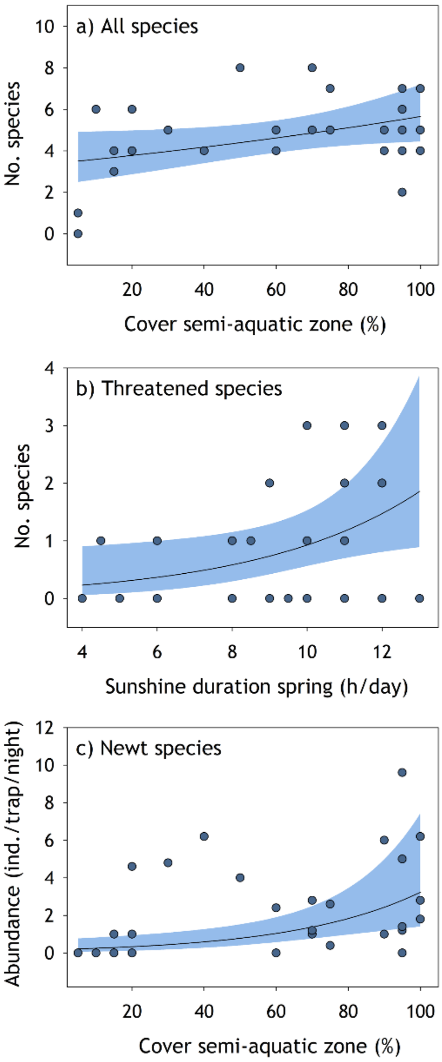

Fig. 5. Relationship between number of all species (a), number of threatened species (b) and newt abundance (c) with significant parameters from the multivariable models ($N = 30$). For statistics see Table 3. (a) y = 0.005038 + 1.228947 × (semi-aquatic zone), $P < 0.05$, $R^2_m = 0.12$, $R^2_c = 0.12$; (b) y = 0.02316 + (–2.39122) × (sunshine duration spring), $P < 0.05$, $R^2_m = 0.16$, $R^2_c = 0.23$; (c) y = 0.028269 + (–0.044221) × (semi-aquatic zone), $P < 0.01$, $R^2_m = 0.32$, $R^2_c = 0.98$. Blue bands indicate 95% confidence intervals. ind. = individuals.

5. Implications for conservation

In quarries, succession is usually delayed due to the lack of topsoil (Münsch and Fartmann, 2022). Additionally, active quarrying regularly creates new and in particular temporary ponds in wheel tracks or excavation depressions and slows down successional speed through driving by construction vehicles (Gilcher and Tränkle, 2005; Baumbach et al., 2013). Such ephemeral ponds are especially important as breeding habitats for *Alytes obstetricans* and *Epidalea calamita* (Günther, 2009). Populations of both species have strongly declined in recent decades (Rote-Liste-Gremium Amphibien und Reptilien, 2020), and quarry ponds are nowadays often the last refuge for the species in our landscapes (this study; Rote-Liste-Gremium Amphibien und Reptilien, 2020). However, due to climate warming, some of the temporary ponds dry out too early in the growing season to enable successful completion of the amphibian metamorphosis (own observation; Streitberger et al., 2016), even for a species with fast development such as *E. calamita* (Günther, 2009). Accordingly, we recommend creating additional ponds in the quarries that contain both large shallow water zones but also some deeper parts to mitigate the negative effects of climate change in the future.

During our study, we regularly detected fresh tracks of raccoons (*Procyon lotor*) at muddy shorelines of the studied ponds and parts of dead amphibians which were likely killed by the species. The racoon is a non-native, omnivorous predator with a strongly growing population in the study area (Klauer and Kriegs, 2015). It has already been shown that especially populations of small mammals, birds and amphibians can strongly suffer from racoon predation (Salgado, 2018; Fiderer et al., 2019). To reduce predation by the raccoon, we recommend installing metal cages above the ponds, at least during the spawning season and around shallow parts of the ponds were amphibians are easily accessible for the species.

Still many reclamation concepts intend to fill, afforest or flood quarries after cessation of mining (Krauss et al., 2009; Tropek et al., 2010). Such measures should generally be prohibited since they do not only have negative effects on amphibians but also many other groups of conservation concern (Beneš et al., 2003; Tropek et al., 2010; Münsch and Fartmann, 2022). Additionally, in abandoned quarries, regular cutting and removal of shoreline vegetation should be implemented to create the preferred early-successional stages (Holtmann et al., 2017). There are many other taxonomic groups that are known to depend on early stages of pond succession und would benefit from such actions (e.g., dragon- and damselflies: Holtmann et al., 2018, 2019a; vascular plants: Holtmann et al., 2019b).

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Appendix

Table A1 Univariable models (Generalized Linear Mixed-effects Models, Poisson error structure): Influence of environmental parameters (predictor variables) on the number of all species, number of threatened species and newt abundance within both pond types (*N* = 30). n.s. = not significant, * *P* <0.05; ** *P* <0.01; *** *P* <0.001.

Parameter	**No. all species**			**No. threatened species**			**Newt abundance**		
	Estimate	**SE**	***P***	**Estimate**	**SE**	***P***	**Estimate**	**SE**	***P***
Habitat quality									
Pond size	5.87×10^{-3}	6.75×10^{-3}	n.s.	1.26×10^{-2}	1.88×10^{-2}	n.s.	1.90×10^{-2}	2.70×10^{-2}	n.s.
Sunshine duration spring	6.99×10^{-2}	3.60×10^{-2}	n.s.	2.32×10^{-1}	1.03×10^{-2}	*	1.56×10^{-1}	7.90×10^{-2}	*
Semi-aquatic zone	5.04×10^{-3}	2.52×10^{-3}	*	1.49×10^{-2}	7.44×10^{-3}	*	2.83×10^{-2}	9.13×10^{-3}	**
Submerged macrophytes	5.67×10^{-3}	3.70×10^{-3}	n.s.	5.61×10^{-3}	1.02×10^{-2}	n.s.	1.41×10^{-2}	1.47×10^{-2}	n.s.
Shrubs	5.45×10^{-3}	6.03×10^{-3}	n.s.	-8.44×10^{-3}	1.77×10^{-2}	n.s.	-3.84×10^{-2}	2.61×10^{-2}	n.s.
Field layer	1.56×10^{-3}	5.72×10^{-3}	n.s.	-4.76×10^{-3}	1.64×10^{-2}	n.s.	-2.30×10^{-3}	2.25×10^{-2}	n.s.
Bare soil	2.74×10^{-3}	3.49×10^{-3}	n.s.	1.55×10^{-2}	8.39×10^{-3}	n.s.	3.08×10^{-2}	2.45×10^{-2}	***
Vegetation height	-2.43×10^{-3}	4.71×10^{-3}	n.s.	-1.73×10^{-2}	1.36×10^{-2}	n.s.	-2.06×10^{-2}	2.14×10^{-2}	n.s.
Landscape quality									
Annual temperature	5.61×10^{-2}	2.11×10^{-1}	n.s.	4.44×10^{-1}	7.43×10^{-1}	n.s.	-10.9×10^{-1}	7.94×10^{-1}	n.s

Table A2 Overview of environmental parameters used for Generalized Linear Mixed-effects Models and their inter-correlations with other environmental parameters (Spearman correlation [r_s], $|r_s| > 0.5$). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Parameter	**Surrogate for** (Spearman Rank Order Correlation [r_s])
Habitat quality	
Habitat type (%)	
Shrubs	.
Field layer	Litter (0.54**), conductivity (–0.51**)
Bare soil	Sunshine duration summer (0.61***), pH (0.53**), trees (–0.50**)
Submerged macrophytes	Conductivity (–0.51**)
Vegetation height (cm)	Trees (0.67***), sunshine duration summer (–0.56**), fish (0.52**)
Pond size (ha)	.
Sunshine duration spring (h/day)	Sunshine duration summer (0.68***), trees (–0.52**)
Semi-aquatic zone (%)	Fish (–0.71***)
Landscape quality	.
Annual temperature (°C)	Elevation (–0.93***), pond connectivity (–0.55**)

Table A3 Summary of PCA results based on the two pond types and environmental parameters (*N* = 30).

Parameter	**Axis**	
	1	**2**
Habitat quality		
Pond size	–0.22	–2.10
Sunshine duration spring	2.91	–1.35
Semi-aquatic zone	2.79	–1.12
Submerged macrophytes	1.95	1.68
Shrubs	–1.04	0.30
Field layer	2.18	3.36
Bare soil	1.75	–3.82
Vegetation height	–3.00	0.78
Landscape quality		
Annual temperature	1.92	1.16
Explained variance (cumulative)	**21.8**	**42.0**

Anhang II: Urkunde – Auszeichnung als UN-Dekade-Projekt

„Biodiversität von Steinbrüchen“

der

Abteilung für Biodiversität und Landschaftsökologie, Universität Osnabrück

wird als offizielles Projekt der
„UN-Dekade Biologische Vielfalt”
ausgezeichnet.

Hürth, 20. Februar 2020

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die UN-Dekade

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