

Terracing in steep slope viticulture and its potential to promote biodiversity in vineyard ecosystems

by

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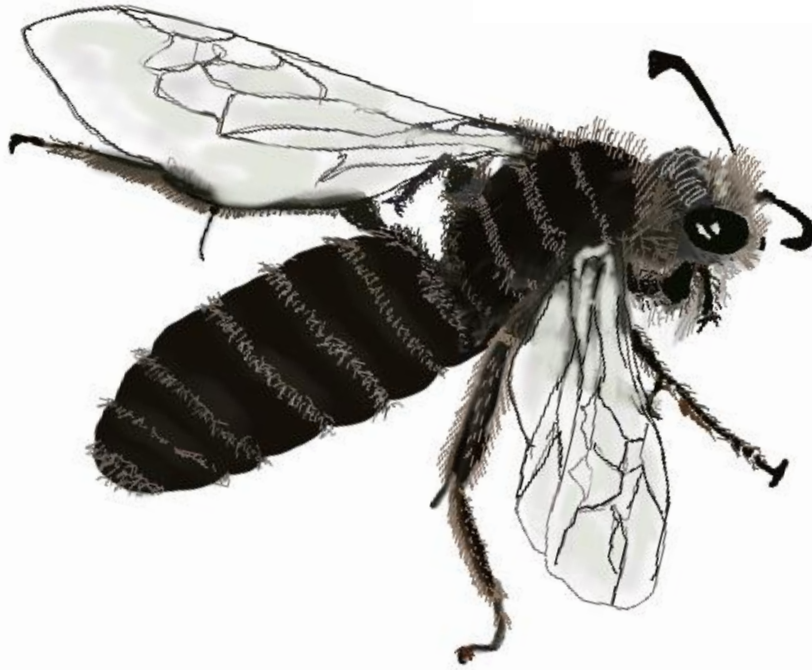
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„Whoever said the small things don't matter
has never seen a match start a wildfire.“

Beau Taplin || Wildfire



Systropha planidens – Artwork by Pia Eibes

Für Sabine.

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Summary

A substantial area of the terrestrial surface is used for agricultural production. In Europe, many farmland species and ecosystems have evolved with traditional agricultural practices and rely on extensive cultivation for their survival. Today, agrobiodiversity is threatened by the abandonment of traditional agricultural land use.

The cultivation of wine is one of the oldest forms of agriculture. On steep slopes, viticulture has shaped landscapes, cultural traditions, and unique ecosystems in many regions. In Germany, steep slope viticulture has been declining dramatically in recent decades due to insufficient profitability. The abandonment of these traditional cultural landscapes threatens the cultural heritage and the flora and fauna adapted to viticultural management. One solution to halt the decline of steep slope viticulture could be a change of cultivation system from vertically oriented rows to modern terraced vineyards. Here, the rows run parallel to the hillside, facilitating cultivation, and thus reducing production costs. At the same time, a large portion of terraced vineyard consists of uncultivated embankments, which can provide valuable habitats within the agricultural system. However, little is known about the effects of a cultivation system change and vineyard abandonment on biodiversity. In addition, information on how to sustainably revegetate terrace embankments is missing.

Within the framework of this dissertation, the overall aim was to evaluate the potential of terraced vineyards to promote biodiversity and investigate measures for sustainable revegetation of terrace embankments. In addition, the effects of distinct vineyard management (vertically oriented vs. terraced) and vineyard abandonment on biodiversity were assessed. The main part of this thesis is based on a field study comparing three vineyard types (vertically oriented vineyard, terraced vineyard, abandoned vineyard) that were arranged in 15 triplets along the Upper Middle Rhine Valley (UMRV) in Germany. The effects of vineyard types, local vineyard parameters, and landscape structure on biodiversity were evaluated using four species groups. Studied groups represented plants and arthropod species (grasshoppers, wild bees, spiders). In a second field study, three newly constructed terrace embankments were revegetated using different seeding techniques and seed mixtures. In addition, measures to support plant establishment were evaluated. Plant establishment was assessed for three consecutive years in permanent vegetation plots.

The first study on the three vineyard types revealed that there was no uniform positive effect of one vineyard type on all investigated groups. Instead, the responses were group and taxon-specific and driven by management-related disturbance intensities, local vegetation structures, soil and landscape structure. In total, the heterogeneous landscape and small-structured vineyard agroecosystem of the UMRV supported high species diversity, hosted high numbers of rare and threatened species, and

diverse species communities across vineyard types. Plant species richness was enhanced by vineyard management and particularly benefited from terraced vineyards and rather nutrient-poor and extensively managed embankments. In comparison, plant communities of fallows were completely different with lower plant diversity. Grasshoppers were supported by vineyard management, and bare ground in vineyard inter-rows supported heat- and open-adapted species. Taller vegetation stands on terrace embankments enhanced grasshopper species richness while woody structures and vineyard abandonment reduced grasshopper diversity and abundance at the local and landscape scale. Wild bee species richness and abundance were strongly determined by their nesting needs. For ground-nesting bees, the suitability of soils for nesting was important, irrespective of vineyard management types whereas above-ground nesting bees were enhanced by woody structures of fallows at the local and landscape scale. Moreover, fallows further provided valuable floral and non-floral resources for both ground- and above-ground nesting bees. For spiders, there was no difference in species richness and abundance between vineyard types but many xerophilic species adapted to open habitat structures prevailed in terraced vineyards. Vineyard fallows supported highly distinct spider communities, including some late-successional species. In conclusion, the vineyard cultural landscape of the UMRV with both actively managed and abandoned vineyards led to a high diversity of plant and arthropod communities. Hence, for its preservation, a spatially heterogeneous landscape comprising both (semi) natural and viticultural-management elements is important.

Results from the second study showed that terraced vineyards and especially terrace embankments can contribute to promoting biodiversity, especially if they are revegetated with regional seed mixtures. Seeds of locally adapted populations and hydro-seeding provided higher vegetation cover which is needed to prevent severe erosion whilst non-locally adapted standard seed mixtures and manual seeding had a higher failure risk and were more prone to severe precipitation events. Taken together, vineyard terracing appears to be a win-win solution for both winegrowers and biodiversity and thus helps to maintain viticulture on steep slopes.

Zusammenfassung

Ein erheblicher Teil der terrestrischen Landoberfläche wird für die agrarwirtschaftliche Produktion genutzt. In Europa sind viele Agrararten und Agrarökosysteme für ihr Fortbestehen auf die extensive landwirtschaftliche Nutzung angewiesen, da sie sich zusammen mit traditionellen landwirtschaftlichen Praktiken entwickelt haben. Agrarbiodiversität ist heute durch die Aufgabe der traditionellen landwirtschaftlichen Nutzung gefährdet.

Der Weinanbau gehört zu den ältesten Formen der Landwirtschaft. Besonders in Steillagen hat der Weinbau in vielen Regionen Landschaften, kulturelle Traditionen und einzigartige Ökosysteme geprägt. In Deutschland ist der Weinbau in Steillagen in den letzten Jahrzehnten jedoch aufgrund mangelnder Rentabilität stark zurückgegangen. Die Aufgabe der Bewirtschaftung in diesen traditionellen Landschaften gefährdet die Kulturlandschaft und die mit der Bewirtschaftung der Weinberge assoziierte Flora und Fauna. Eine Lösung, um dem Rückgang des Steillagenweinbaus entgegen zu wirken, könnte die Umstellung des Anbausystems von in Falllinie gezeilten Reben hin zu modernen Querterrassenweinbergen sein. Hier verlaufen die Weinbergsgassen hangparallel, was die Bewirtschaftung erleichtert und die Produktionskosten senkt. Gleichzeitig besteht ein großer Teil der Querterrasse aus Böschungen, die unbewirtschaftet bleiben und wertvolle Lebensräume innerhalb des landwirtschaftlichen Systems darstellen. Über die Auswirkungen einer veränderten Bewirtschaftungsform und der Nutzungsaufgabe im Steillagenweinbau auf die Biodiversität ist jedoch wenig bekannt. Darüber hinaus fehlen Informationen darüber, wie Querterrassenböschungen nachhaltig begrünt werden können.

Das übergeordnete Ziel dieser Dissertation war, das Potenzial von Querterrassenweinbergen zur Förderung der Biodiversität zu evaluieren und Maßnahmen zur nachhaltigen Begrünung von Querterrassenböschungen zu untersuchen. Darüber hinaus wurden die Auswirkungen einer unterschiedlichen Bewirtschaftung der Weinberge (Falllinie vs. Querterrasse) und der Aufgabe der weinbaulichen Nutzung auf die Biodiversität untersucht. Der Hauptteil dieser Arbeit basiert auf einer Feldstudie, die das Potential für die Biodiversität über drei Weinbergstypen (Falllinie, Querterrasse, Weinbergsbrache) hinweg vergleicht. Die drei Weinbergstypen waren in 15 Triplets entlang des Oberen Mittelrheintals in Deutschland angeordnet. Die Auswirkungen der Weinbergstypen, der lokalen Weinbergparameter und der Landschaftsstruktur auf die Biodiversität wurden anhand von vier Artengruppen bewertet: Pflanzen und Arthropodenarten (Heuschrecken, Wildbienen, Spinnen). In der zweiten Feldstudie zur Böschungsbegrünung wurden Böschungen von drei neu angelegten Querterrassenweinbergen mit unterschiedlichen Aussaattechniken und Saatgutmischungen begrünt und Maßnahmen zur Förderung der Anfangsetablierung untersucht. Die Etablierung der Vegetation wurde in drei aufeinanderfolgenden Jahren in permanenten Vegetationsplots bewertet.

Die Ergebnisse der vergleichenden Studie der drei Weinbergstypen haben gezeigt, dass nicht ein einzelner Weinbergstyp einen positiven Effekt auf alle untersuchten Gruppen hatte, sondern, dass die Reaktionen gruppen- und taxonspezifisch waren und durch die Intensität der mit der Bewirtschaftung verbundenen Störungen, lokalen Vegetationsstrukturen, sowie Boden- und Landschaftsstrukturen bestimmt wurden. Insgesamt hat die heterogene Landschaft und das kleinstrukturierte Agrarökosystem des Oberen Mittelrheintals zu einer hohen Biodiversität mit vielen seltenen und gefährdeten Arten sowie diversen Artengemeinschaften über die verschiedenen Weinbergstypen hinweg, beigetragen. Die Bewirtschaftung der Weinberge erhöhte die Pflanzendiversität, die besonders von den Querterrassen und deren nährstoffärmeren und extensiv bewirtschafteten Böschungen profitierte. Die Pflanzengemeinschaften der Brachen unterschieden sich deutlich von den bewirtschafteten Weinbergen und hatten insgesamt eine niedrigere Diversität als diese. Die Heuschrecken profitierten von der Bewirtschaftung und der dadurch geschaffene Offenboden in den Weinbergsgassen begünstigte wärmeliebende Offenland-Arten. Der Artenreichtum der Heuschrecken wurde durch höheren Vegetationsbestände der Böschungen gefördert, während holzige Strukturen und die Nutzungsaufgabe die Diversität und Abundanz der Heuschrecken auf der lokalen und Landschaftsebene reduzierten. Die unterschiedlichen Nistbedürfnisse waren für den Artenreichtum und die Abundanz der Wildbienen ausschlaggebend. Für bodennistende Bienen spielten die Eigenschaften des Bodens, unabhängig von der Bewirtschaftungsform, eine wichtige Rolle, während oberirdisch nistende Bienen von Gehölzstrukturen in den Weinbergsbrachen sowohl auf lokaler als auch auf der Landschaftsebene profitierten. Brachflächen boten darüber hinaus wertvolle florale und nicht-florale Ressourcen sowohl für boden- als auch für oberirdisch nistende Bienen. Für den Artenreichtum und die Abundanz der Spinnen gab es keine Unterschiede zwischen den Weinbergstypen, aber xerophile Arten, die an offene Lebensraumstrukturen angepasst sind, überwogen in den Querterrassen. In den Weinbergsbrachen fand sich eine von den Weinbergen abweichende Spinnengemeinschaft, die viele Arten später Sukzessionsstadien aufwies.

Zusammenfassend lässt sich sagen, dass die Weinbergskulturlandschaft des Oberen Mittelrheintals mit sowohl aktiv bewirtschafteten als auch aufgegebenen Weinbergen eine hohe Diversität von Pflanzen- und Arthropodengemeinschaften aufweist. Für ihre Erhaltung ist daher eine räumlich heterogene Landschaft wichtig, die sowohl (halb)natürliche als auch weinbaulich bewirtschaftete Teile umfasst. Die Ergebnisse der zweiten Studie haben gezeigt, dass Querterrassen hierzu und insbesondere, wenn sie mit regionalen Saatgutmischungen begrünt werden, einen Beitrag leisten können. Saatgut lokal angepasster Populationen und Nassansaat sorgten für eine höhere Vegetationsbedeckung, die erforderlich ist, um starke Erosionsschäden zu verhindern, während nicht lokal angepasste Standardsaatgutmischungen und Handansaat ein höheres Ausfallrisiko hatten und anfälliger für starke

Niederschlagsereignisse waren. Insgesamt scheint die Terrassierung von Weinbergen eine Lösung zu sein, von der sowohl die Winzer als auch die Biodiversität profitieren und die somit zur Erhaltung des Weinbaus in Steillagen beitragen kann.

1. Introduction

The general aim of the present thesis was to evaluate the potential of terraced vineyards in promoting biodiversity and to investigate measures for sustainable revegetation of terrace embankments. In addition, the effects of distinct vineyard management (vertically oriented vs. terraced) and vineyard abandonment on biodiversity were investigated.

At first, agriculture and its impacts and relation to biodiversity in the past and the present are shortly portrayed. Subsequently, measures and concepts to support biodiversity in agroecosystems are outlined. Viticulture in general and viticulture on steep slopes in particular as well as its potential for biodiversity are discussed and the concept of vineyard terracing is introduced. In the end, the study area and field study designs are described and a brief overview of the studied organism groups is given. In the following chapters, specific species groups and aims targeted are presented in detail.

1.1 Threats to biodiversity in agricultural landscapes

Almost 40 % of the world's terrestrial surface is covered by agricultural land (FAOSTAT 2022) that provides multiple services for people such as the production of food, fibre, fuels and rural livelihoods (Hart et al. 2016; Galler et al. 2015; Foley et al. 2005). Historically, small-scale and low-intensity agriculture in Europe has resulted in patchworks of habitats favourable to many species and species-rich communities (Sutcliffe et al. 2015; Kleijn et al. 2009; Bignal and McCracken 1996). Many farmland species and ecosystems have evolved with traditional agricultural practices and thus rely on cultivation for their survival (Hampicke 2006).

Since the early 20th century, the development and large-scale application of synthetic fertilizers and pesticides and an increasing mechanization level have led to more intensive and higher-yielding agricultural production (Batáry et al. 2020). This development is a serious threat to biodiversity and ecosystem functions (Tscharntke et al. 2012; Benton et al. 2003; Robinson and Sutherland 2002). Agricultural intensification affects biodiversity at two distinct but mutually connected scales: At the local scale, intensification negatively affects the ecological quality of agricultural fields as habitats through increased application of agrochemicals (pesticides and fertilizers), deep ploughing, massive use of machinery, and modified rotation schemes (e.g. earlier and more frequent mowing of meadows) (Storkey et al. 2012; Stoate et al. 2009). At the landscape scale, agricultural intensification has led to habitat fragmentation, the loss of highly valuable habitats such as semi-natural pastures, wetlands, and residual habitats, and landscape simplification i.e. increased field size with fewer crops (Fahrig et al. 2015; Tscharntke et al. 2012). In other words, agricultural intensification is threatening agrobiodiversity through the ongoing conversion and simplification of once heterogeneous structures at the local and landscape scale (Tscharntke et al. 2005; Benton et al. 2003). Agro-ecological literature emphasizes that

this has greatly contributed to the current biodiversity crisis in Europe and is leading to a decline in ecosystem services such as crop pollination, biological pest control, and nutrient recycling (Sutcliffe et al. 2015).

While there is widespread public awareness of the negative impacts of agricultural intensification on biodiversity, agricultural abandonment receives less attention but contributes to European farmland biodiversity decline, too (Ustaoglu and Collier 2018). In traditional land-use systems, agriculture even promotes species and habitat richness (Plieninger et al. 2006). Consequently, management cessation at these sites reduces overall biodiversity and changes species composition in the long-term (e.g. heathlands (Rosa García et al. 2013); calcareous grasslands (WallisDeVries et al. 2002), forest pastures (Horák et al. 2018)). However, the consequences of agricultural abandonment are still debated as the results of the studies are contrasting and dependent on the conservation value of the area, agro-climatic conditions, and local as well as regional factors (Ustaoglu and Collier 2018; Queiroz et al. 2014; Benayas et al. 2007). Hence, abandonment of agricultural fields can contribute to habitat regeneration and restoration (e.g. native forests (Aide et al. 2013)) but then again cause the loss of farmland species (e.g. birds (Kamp et al. 2018)).

Overall, agricultural intensification remains the main trend in productive areas and on fertile soils, but on marginal sites with poor soils or sites that are difficult to cultivate (e.g. hilly or mountainous regions) (Paz et al. 2023; Marini et al. 2011) farmland abandonment and reforestation have increased (Cramer et al. 2008). Nevertheless, both trends alter habitat conditions and threaten agrobiodiversity in their own way.

1.2 Concepts to protect agrobiodiversity

Today, agrobiodiversity is considered just as important as “wild biodiversity” (Phillips 1998) and is not perceived as something “nice to have” without any economic benefit for farmers anymore. Instead, it is known as something essential for stable, productive, and functioning farming systems (Scherber 2022).

There has been a debate among conservationists and ecologists on whether biodiversity is better preserved by segregating conservation from agricultural production (land-sparing) or by combining agricultural management and nature conservation (land-sharing) (Grass et al. 2019; Balmford et al. 2019; Fischer et al. 2014). The land-sparing concept focuses on species that are incompatible with agriculture and need pristine and undisturbed areas to persist (Gámez-Virués et al. 2015; Green et al. 2005). This is particularly true for many species native to tropical landscapes where agricultural expansion destroys unique ecosystems (Laurance et al. 2014) and for species with high habitat specialization and low dispersal ability (Tscharntke et al. 2012). On the contrary, land-sharing focuses

on species adapted to agricultural production that depend on biodiversity-friendly cultivation as they use the agricultural matrix for foraging and reproduction (Grass et al. 2019; Phalan et al. 2011). Land-sharing is particularly important in European agricultural landscapes due to the dependence of farmland biodiversity on traditional cultivation (Batáry et al. 2020). At the landscape scale, maintaining heterogeneous agricultural landscapes has been identified as a key measure to preserve and promote agrobiodiversity (Benton et al. 2003). In general, structurally rich and complex landscapes have high biodiversity (Tscharntke et al. 2005), but not all functional groups equally respond to and profit from landscape heterogeneity (Martin et al. 2019). The compositional heterogeneity of a landscape (diversity and abundance of habitat types) and the configurational heterogeneity (spatial alignment, position, or orientation of landscape features) are essential to facilitate species movements, avoid species extinctions in spared natural habitats and promote species spillover (Grass et al. 2021; Fahrig 2013; Batáry et al. 2011). Hence, to preserve agrobiodiversity, multifunctional landscapes are needed that include elements from both land-sparing and land-sharing (Grass et al. 2021).

The protection of agrobiodiversity has become a key issue of the first pillar of the European Common Agricultural Policy (CAP) and numerous European countries have implemented national agricultural and environmental policies for biodiversity conservation like agri-environment schemes (AES) (Pardo et al. 2020; Pe'er et al. 2019). AES are incentive-based instruments that aim to counteract the negative effects of agricultural intensification on ecosystems by providing compensation payments to farmers for adopting or maintaining wild-life friendly and input-reducing farming practices (Batáry et al. 2015; Villanueva et al. 2015; Uthes and Matzdorf 2013). Most AES are management agreements such as organic farming, reduced use of fertilizer and pesticide application rates, crop rotations and diversification but also landscape and habitat measures (van Vooren et al. 2017; Hiron et al. 2013).

Former CAP instruments to support farmland biodiversity included the conservation of permanent grassland and the creation or maintenance of ecological focus areas (EFAs) (Pe'er et al. 2017). In general, CAP-instruments and AES promote agrobiodiversity but their success is dependent on several factors such as the regional and landscape context and the correct realization and management of implemented measures (Batáry et al. 2015; Berendse et al. 2014). In addition, AES primarily favour common and widespread species while rare and threatened species only rarely benefit (Kleijn et al. 2006). To support rare and threatened species, management restrictions within AES are often not sufficient because they do not address species-specific needs and their spatial distribution and require expert advice for successful management (Batáry et al. 2015). The CAP's effectiveness has been questioned by ecologists and CAP instruments and AES have been criticized for setting requirements that are too low to halt the loss of farmland biodiversity (Pe'er and Lakner 2020; Whittingham 2007; Berendse et al. 2004; Kleijn and Sutherland 2003). For example, AES are often not too demanding,

require little resource investment and are designed to easily fit into production to increase farmers' acceptance (Batary 2015). In addition, measures (e.g., flower strips) are implemented by individual farmers but would be more effective when designed in a network that guarantees temporal continuity and spatial connectivity (Boetzi et al. 2021). Alternative examples from the Netherlands show that collectively performing AES in a regional approach can make AES more ecologically sustainable (van Dijk et al. 2015).

1.3 Viticulture

In Europe, permanent crops (e.g. fruit orchards, olive groves, vineyards) represent the third most widespread agricultural system and cover about 6 % of the cultivated surface (Iglesias et al. 2012). Among permanent crops, vineyards are of high economic value with approximately 7.3 million hectares of grapevines planted globally, of which ca. 50% are located in Europe (OIV 2021). In some high-producing wine countries such as France or Italy, vineyard area accounts for 20 % of the agricultural production area, while in Germany vineyard areas are relatively small (0.6 %; 103 421 ha) compared to other crops (OIV 2021). Globally, grapes are used for wine (approx. 49%), table grapes (approx. 43 %), and dried grapes (approx. 8%) (OIV 2021).

As a perennial agricultural system and with wine production being part of the historical and cultural heritage of many regions, viticulture has contributed to shaping the appearance of landscapes, cultural traditions and unique ecosystems (Assandri et al. 2018; Winkler and Nicholas 2016) (Figure 1 A) of which many have been designated UNESCO World Heritage Sites (UNESCO 2022) (e.g. Piedmont in Italy, Burgundy in France; Alto Douro Valley in Portugal). Yet, vineyards, similarly to other agricultural systems, are globally experiencing strong management intensification and expansion (Paiola et al. 2020; Viers et al. 2013). In the past decades, severe intensification by the increased use of agrochemicals, intensive tillage, increased field sizes, low cultivar density and the removal of traditional elements (e.g. dry-stone walls) has led to featureless and homogeneous vineyard landscapes (Rusch et al. 2021; Paiola et al. 2020; Wolkovich et al. 2018) (Figure 1 B). The simplification of previously complex vineyard landscapes negatively affects biodiversity across taxa (Viers et al. 2013). For instance, in simplified vineyard landscapes cavity-nesting bee species richness and abundance were lower (Uzman et al. 2020) and the reduction of natural habitats has caused declines in bird species in vineyard landscapes in California (Jedlicka et al. 2011), Chile (Steel et al. 2017), and Switzerland (Sierro et al. 2001). Along with intensification, vineyard expansion mainly proceeds at the expense of natural habitats and associated biodiversity (Paiola et al. 2020), especially in regions with a Mediterranean climate such as South Africa, Chile, or California and upwards in mountain areas. In the Cape Floristic region, South Africa, vineyard expansion has destroyed valuable vegetation types (fynbos and

1. Introduction

renosterveld) and threatened endemic plant species (Fairbanks et al. 2004) while in California vineyard expansion has led to the destruction of grasslands and oak woodlands (Merenlender 2000).

Often planted in large-scale monocrops, vines are subject to several pests and diseases and require intensive management with high plant protection frequencies to maintain crop health and productivity (Pertot et al. 2017). The average number of pesticide treatments per year depends on pedoclimatic conditions and varies considerably across years but between 10 and 20 pesticide applications per year (up to 30) are common (Pertot et al. 2017). Among pesticides, fungicides account for approx. 80 % to control common fungal diseases such as downy mildew (*Plasmopara viticola*), powdery mildew (*Erysiphe necator*) or grey mould (*Botrytis cinerea*). Insecticides against common arthropod grapevine pests such as the grapevine moths (e.g. *Lobesia botrana*) or leafhoppers (e.g. *Empoasca vitis* and *Scaphoideus titanus*, vector of the Flavescence Doree phytoplasma), as well as herbicides, are less frequently applied (Rusch et al. 2021).

In Europe, vineyard expansion and management intensification are particularly worrying because permanent crops were considered environmentally sustainable and were thus excluded from the greening obligation in the CAP reform (Assandri et al. 2016). It is up to the member states and local governments to define adequate measures to support sustainable and environmentally friendly farming practices in viticulture and to counteract biodiversity loss. In Germany, at the federal-state level, very few measures to support environmentally friendly viticultural management, exist (e.g. synthetic moth pheromones instead of insecticide application) (HMUKLV 2020). Therefore, farmers' incentives to conserve and support biodiversity in vineyards are diminished due to insufficient financial compensation (Assandri et al. 2017).

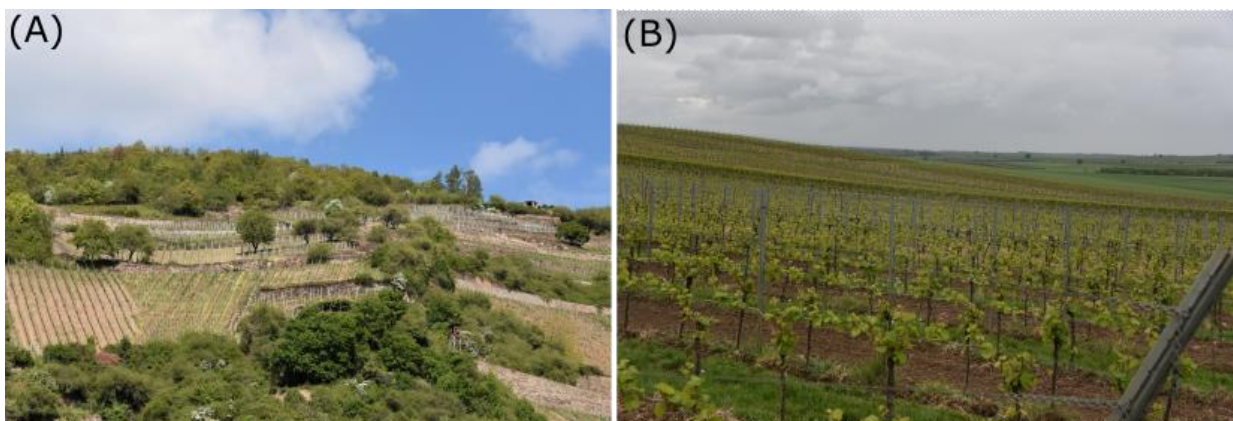


Figure 1: Pictures show examples of traditionally managed and structurally rich (A) and intensified and homogeneous (B) vineyard landscapes in Germany. Pictures by K. Mody.

1.4 Biodiversity potential of vineyards

Viticultural landscapes used to be one of the most species-rich landscapes composed of a mosaic of small vineyards, semi-natural habitats like fallows or field margins, stone walls, and hollow ways that provided valuable habitats for many thermophilous species (Poschlod and Braun-Reichert 2017). At present, increasing vineyard area often has negative effects on biodiversity, primarily by the loss of habitats (Petrescu Bakış et al. 2021). However, in contrast to annual cropping systems, disturbance levels in vineyards are lower (Bruggisser et al. 2010), which potentially turns these into rather stable and attractive habitats for a range of species, particularly when vineyard inter-rows are covered by native vegetation or diverse cover crops (Eckert et al. 2020; Winter et al. 2018). In temperate regions, permanent vegetation usually covers each second inter-row, while the other one is kept bare by regular tillage. In Mediterranean regions, all inter-rows are kept bare by tillage or herbicide applications mainly for reasons of water competition and scarcity (Garcia et al. 2018). Inter-row vegetation management depends not only on climate but also on soil type, grape variety and winegrowers' management approach (Winter et al. 2018).

Well-adjusted inter-row management is a key measure to support biodiversity in vineyards (Brambilla and Gatti 2022; Geldenhuys et al. 2021). Careful mechanical disturbance and soil tillage are essential to maintain vineyard geophytes like *Muscari neglectum*, *Gagea villosa*, and *Allium vineale*, which struggle to compete with dense inter-row vegetation and cover crops (LWG 2022). Yet, extensive management practices or sowing of biodiversity-friendly seed mixtures in inter-rows have not been included in AES in Germany.

Vineyard inter-rows have been suggested to support species related to open habitats such as the Woodlark *Lullula arborea* and their invertebrate prey (Bosco et al. 2019; Arlettaz et al. 2012) or even provide potential surrogate habitats for species typical for dry calcareous grasslands (Ortis et al. 2021; Nascimbene et al. 2016). However, these studies were performed in hilly and rather traditionally managed areas that might comprise a higher biodiversity potential. Hilly vineyard landscapes are often characterized by distinctive biophysical features that have a particularly high value for rare and xero-thermophilic habitat specialists because the harsh topography prevents intensive mechanization and intensification (Assandri et al. 2018).

Biodiversity potential of vineyards is also tied to structural elements like hedgerows, dry stone walls, isolated large trees and hollow ways that contribute to habitat heterogeneity at the landscape scale and thus fulfil the distinct ecological requirements for species during their different life stages (Assandri et al. 2018; Kelly et al. 2016). To sum up, viticultural landscapes potentially support species-rich

communities, but the quality of the vineyard habitat highly depends on management intensity and habitat heterogeneity at the local and landscape scale.

1.5 Steep slope viticulture

Historically and under cooler climate conditions, planting vines on steep slopes has enabled viticulture in climatically marginal zones to produce best quality wines due to their distinctive microclimate, especially during the ripening period (Hoppmann et al. 2017). In addition, this practice has made use of otherwise unsuitable agricultural land, as flat fertile fields have been reserved to produce arable crops (Petit et al. 2012). However, the cultivation on steep slopes is known to cause high rates of runoff, soil and nutrient loss which have been overcome by building terraces made of dry-stone walls or earth banks to reduce slope length (Pijl et al. 2020; Tarolli et al. 2014). In Europe, this small-scale terracing has contributed to creating unique agroecosystems with high conservation and cultural value (UNESCO 2022; Tieskens et al. 2017).

Today, steep slope viticulture is facing several challenges of which the largest might be the cost disadvantage in comparison to flat terrain sites. On steep slopes, mechanization is often difficult and complex leading to high manpower requirements and thus higher production costs (Lourenço-Gomes et al. 2015). Market prices of wines produced on steep slopes and subsidies for steep slope cultivation do not cover additional expenses (Loose and Strub 2017). This has led to a substantial decline in traditionally managed vineyard areas throughout Europe. In the Alto Douro Valley (Portugal) traditionally managed acreage has decreased by 29 % (2001 - 2012) (Lourenço-Gomes et al. 2015) while in the Mosel Valley in Germany, the viticultural acreage on steep slopes has declined by up to 25 % since 1999 (State Statistical Office of Rhineland-Palatinate 2021). Subsequent responses to the high maintenance costs of steep slope cultivation are either intensification of management (Figure 2 A) or abandonment of marginal and less productive sites (Figure 2 B). Management intensification includes changes in the training system e.g. in 'spalliera' system (Assandri et al. 2018). Further, within land consolidation processes small terraces are being replaced by vines planted in a downhill direction (vertically oriented hereafter) (Lourenço-Gomes et al. 2015). Despite simplified work due to an increase in the mechanization level, the labour demand on steep slopes is still estimated to be two to six times higher than on flat terrain sites (Schrieck 2016). In addition, under warming climate conditions, the risk of drought is increasing, turning the former advantages of steep slope vine cultivation into a disadvantage (Fraga 2020).

1. Introduction



Figure 2: Trends in steep slope viticulture (A) intensification by vertically oriented rows and (B) abandonment with following succession of vegetation.

Both trends, intensive use of productive sites and agricultural abandonment with subsequent shrub encroachment on marginal sites threaten habitat quality for the flora and fauna adapted to extensive viticultural management and potentially turn diverse and fairly nutrient-poor cultural landscapes into rather homogeneous ones, in which once typical elements such as dry-stone walls can now only be found in fragments (Tieskens et al. 2017). On that account, vineyard management alternatives are required to overcome the economic disadvantages of steep slope viticulture and meet environmental challenges (e.g., climate change) to maintain management to preserve valuable cultural landscapes, and associated biodiversity and secure the livelihood of local winegrowers.

1.6 Terracing in steep slope viticulture

One approach to keep management economically viable and thereby halt the decline of viticulture on steep slopes could be the construction of modern, drivable vineyard terraces (Figure 3). This has been done in the Alto Douro Valley, but also in Priorat in Spain, the Baden Kaiserstuhl area in Germany and more recently in the UMRV in Germany. Modern vineyard terraces (referred to as vineyard terraces hereafter) are being constructed via a ‘cut and fill’ procedure where a caterpillar levels the platforms along the slope’s contour line and compacts the soil and an excavator forms the embankments (Strack et al. 2021). The vines are usually planted in a single row at the edge of the platform. Hillside parallel terraces help reduce production costs by facilitating mechanization, accelerating manual work steps, and improving occupational safety (Strub and Loose 2021). In relation to the total vineyard area, vine density/m² at terraced vineyards is lower compared to vertically oriented vineyards, but yields per vine (litre/vine) appear to be similar (personal communication A. Laquai).

A substantial area of terraced vineyards is composed of embankments that are managed extensively (no fertilizer or pesticide application, low disturbance level), and can provide valuable habitats for xerothermophilic communities (Košulič et al. 2014). Embankments further contribute to reducing the

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risk of erosion and nutrient loss and increase the water retention capacity, especially in winter (Strack and Stoll 2022). Nevertheless, terraces must be constructed and maintained properly since poorly managed and insufficiently stabilized embankments may lead to collapses of the terrace and an increase in soil erosion (Pijl et al. 2020; Rodrigo-Comino et al. 2019). For this purpose, vegetation, growing on embankments not only improves stability but also improves soil physical and chemical characteristics and enhances habitat quality. However, recommendations for practitioners on how to revegetate embankments are currently missing.



Figure 3: Modern terraced vineyards facilitate management and lower production costs while terrace embankments remain uncultivated and provide habitats within the viticultural system.

For vineyards and biodiversity to mutually profit from one another, it is essential to integrate economically and ecologically compatible viticultural practices. Terraced vineyards could master this challenge because embankments have enormous potential to serve as habitats within the viticultural systems and might even contribute to habitat networking. However, the specific potential of terraced vineyards and their role in providing habitats for various species groups remain insufficiently explored.

This thesis aims to evaluate the potential of vineyard terracing to promote biodiversity in the context of maintaining economically viable viticultural management on steep slopes and assess the effects of vineyard abandonment on biodiversity.

In this regard, the following research questions are defined:

1. How do different vineyard management types (vertically oriented vs. terraced vineyard), abandoned vineyards and the landscape structure effect the diversity, abundance and community composition of plants and different arthropod groups?
2. How can newly constructed terraced vineyards be revegetated sustainably and with high ecological benefit?

2. Study design and research outline

2.1 Study area and methods

The Upper Middle Rhine Valley (UMRV) in Germany was chosen as the study area because here, viticulture on steep slopes has a long tradition and has shaped an ancient cultural landscape with high conservation value that has been seriously threatened by management cessation in the past decades (Veith et al. 2012). The cultural landscape of the UMRV is a UNESCO World heritage site and part of the German Biodiversity hotspot ‘Middle Rhine valley with its side valleys Nahe and Mosel’ (Ackermann and Sachteleben 2012). It is characterized by a dry and warm climate with a high diversity of habitats and xerothermophilic species of conservation concern (Ackermann and Sachteleben 2012).

In the UMRV, vines were traditionally planted on small terraces made of dry-stone walls but during land consolidation measures in the 1960s this small structured cultivation was merged into large vineyard sites with vertically oriented rows to increase productivity and mechanization levels (Treiling 2008). However, due to the cost disadvantages of steep slope viticulture, steep slope vineyards have increasingly been abandoned in the past decades in the Middle-Rhine Valley (up to 39%; 1987–2019) (Stoll and Schultz 2020). Of the former 2500 ha in 1909, only about 450 ha of cultivated vineyard area remains today (State Statistical Office of Rhineland-Palatinate 2021). This development does not only threaten the income of the local winegrowers, but the progressive expansion of fallow land and ongoing succession also endanger the preservation of the cultural heritage and its associated flora and fauna. In the past years, some winegrowers have changed their cultivation system from vertically oriented rows to modern terraced vineyards. This change in cultivation practices formed the basis of this thesis and gave the idea for the BioQuiS-project funded by the German Environmental Foundation [34025/01].

In this thesis, the term “vineyard management” refers to maintaining open habitat structures and counteract shrub encroachment on steep slopes. The need to reduce high plant protection frequencies is only marginally addressed here, as the focus lies on maintaining viticultural management. The term “managed vineyards” includes vertically oriented and terraced vineyards while “vineyard types” includes all three investigated vineyards: vertically oriented, terraced, and abandoned (Figure 4).

2. Study design and research outline

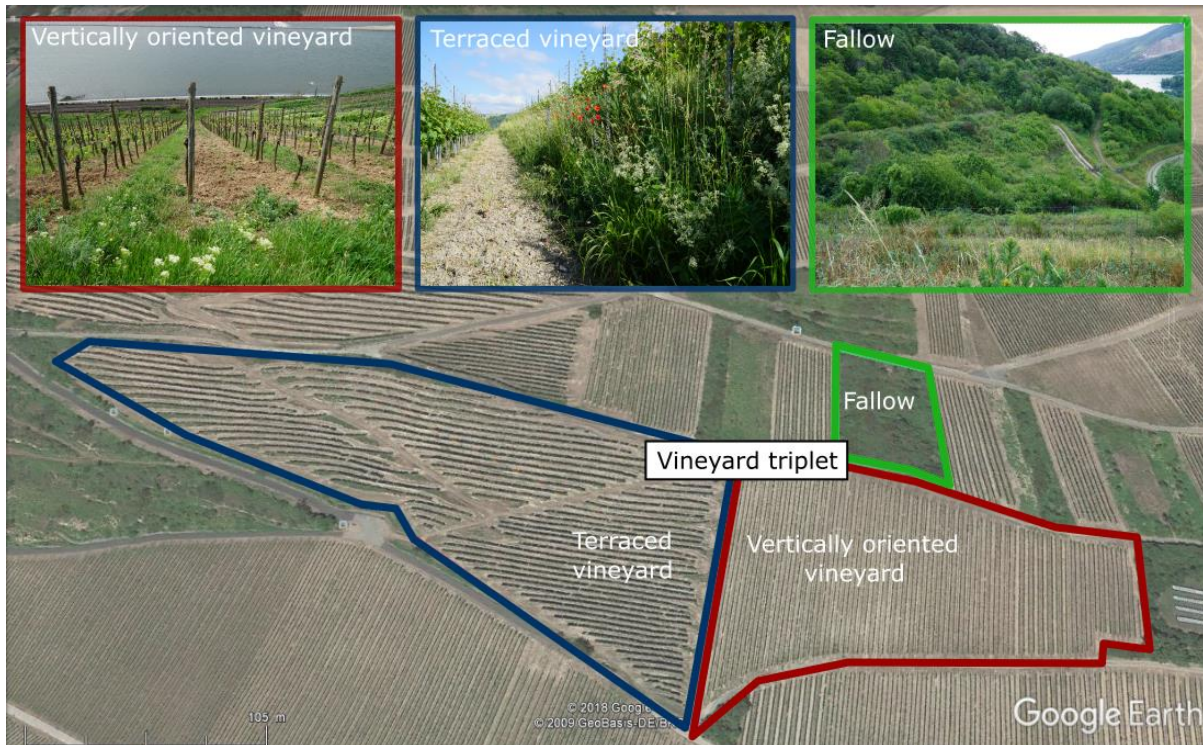


Figure 4: Three vineyard types were studied and arranged in triplets to be in close vicinity to each other and to represent comparable environmental conditions. Each triplet included a vertically oriented vineyard (red), a terraced vineyard (blue) and a vineyard fallow (green). Vertically oriented vineyards had an alternating tillage treatment, i.e., every second inter-row was tilled while the other was permanently covered with vegetation. Terraced vineyard embankments were extensively managed and permanently covered with vegetation. Inter-rows of terraced vineyards were tilled. Vineyard fallows were not managed and abandoned for at least 10 years.

Within the framework of this thesis, two main field studies were set up to address the research objectives. For the first study regarding the comparison of vineyard management types and abandoned vineyards, four species groups representing distinct taxonomic and trophic groups were chosen: plants (habitat and food provision), grasshoppers (herbivores and prey), wild bees (pollinators), and spiders (soil-dwelling predators). All studied organism groups are commonly used ecological indicators with well-established sampling methods and well-known ecological behaviour (Gerlach et al. 2013; Ellenberg 1996). From 2018 to 2020, organism groups were sampled in 15 vineyard triplets along the UMRV, each including a terraced vineyard, a vineyard with vertically oriented rows and a vineyard fallow adding to a total of 45 study sites (see triangles in Figure 5 for triplet locations; Figure 4 for vineyard types).

2. Study design and research outline

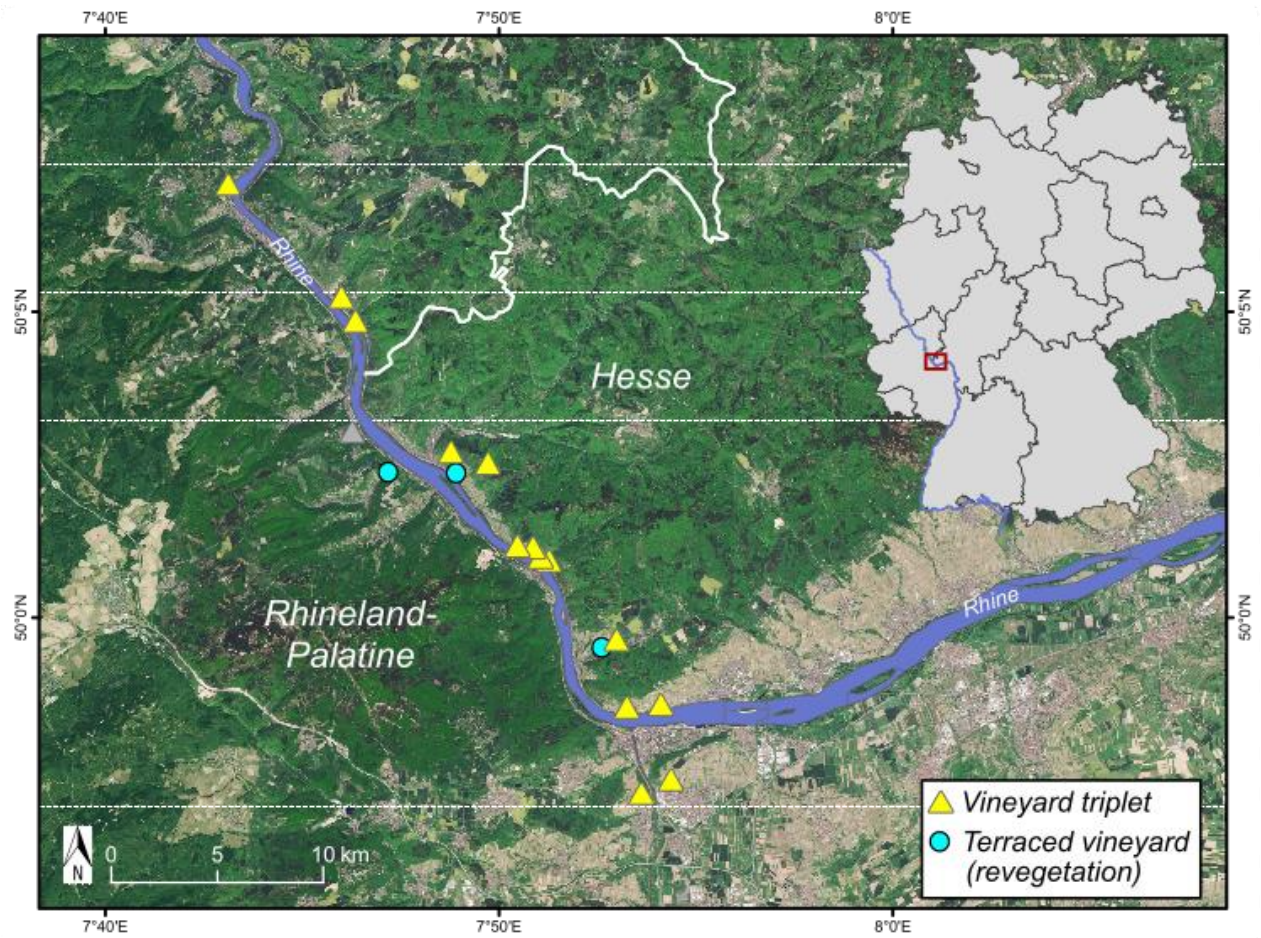


Figure 5: Overview of vineyard locations in the UMRV in Hesse and Rhineland-Palatinate, Germany chosen for the two main field studies embedded within the BioQuis-project. For the comparison of vineyard types, 15 vineyard triplets (yellow triangles) were chosen. Each vineyard triplet comprised a vertically oriented vineyard, a terraced vineyard and a vineyard fallow. Light blue dots represent newly constructed terraced vineyards used to study the revegetation of terrace embankments.

2. Study design and research outline

For each organism group, relevant local environmental (e.g. cover of bare ground) and management parameters (e.g. inter-row management) were assessed in each vineyard, and for the arthropods, the landscape structure within a radius of 150 metres around the study sites was characterized. Further ecological background and methodological details are given in the respective chapters, but as a first overview, Figure 6 shows the studied organism groups and sampling methods.

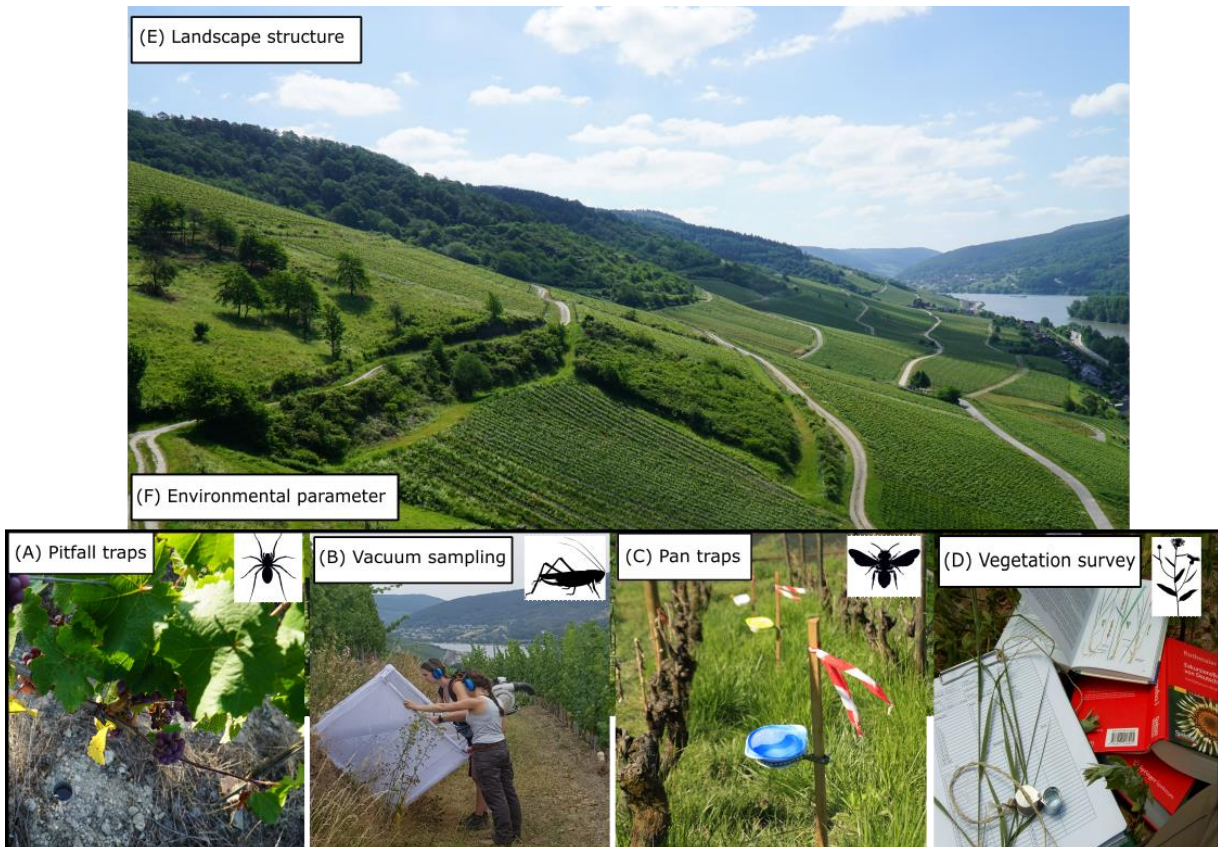


Figure 6: Overview of organism groups and respective sampling methods (A-D) investigated in the field studies comparing vineyard types (vertically oriented vineyards, terraced vineyards, and abandoned vineyards). Relevant landscape (e.g. cover of SNH) and environmental parameters (e.g. cover of bare ground) were assessed for each investigated group (E-F). Pictures by V. Wersebeckmann (A,D), C. Biegerl (B) and C. Reiß (C). Icons by C. Reiß.

2. Study design and research outline

For the second study to investigate how terrace embankments can be revegetated sustainably, three newly constructed terraced vineyards were revegetated in 2018. At each vineyard, two seeding techniques (manual vs. hydro seeding), three seed mixtures (regional seeds, hay threshing, commercial seeds) and supporting measures for the establishment of the vegetation on the embankments (nurse species, hay mulch, fertilizer) were investigated in a nested design. The performance and suitability of seeding techniques, seed mixtures and supporting measures were evaluated within permanent vegetation plots surveyed from 2018 – 2020. Figure 7 gives an overview of the main aspects addressed in the revegetation study.

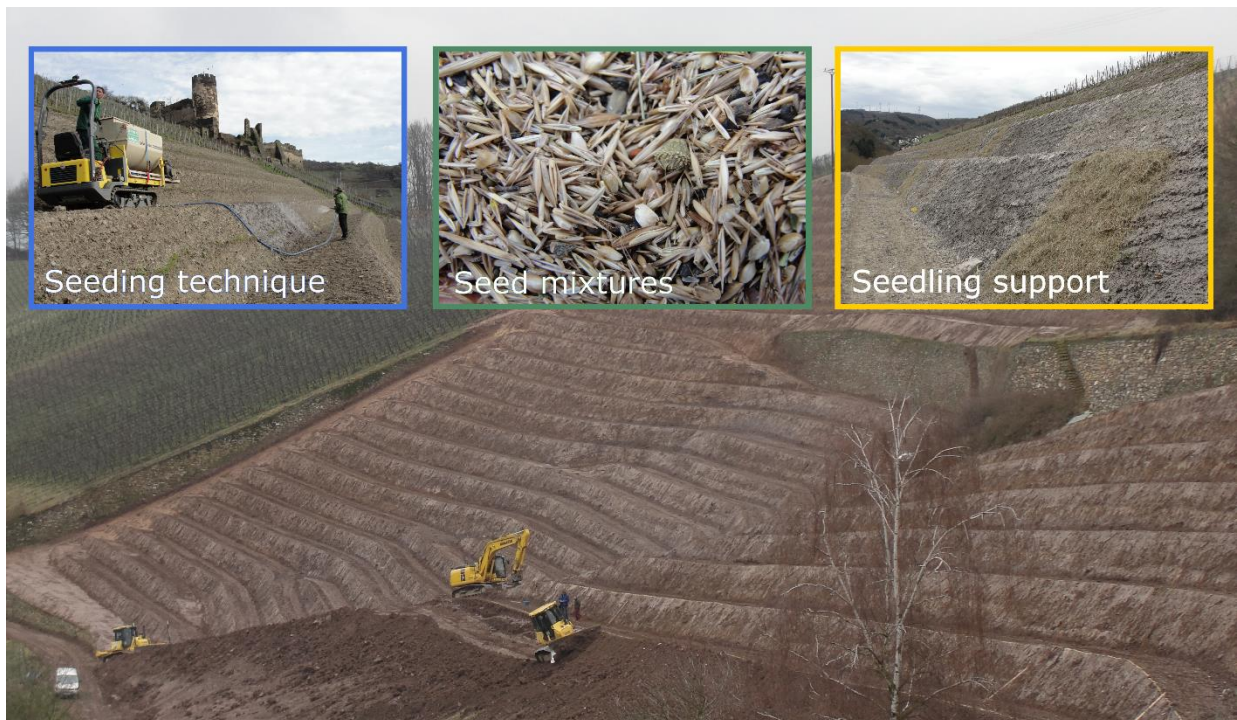


Figure 7: Pictures show the construction of a terraced vineyard and the main aspects (boxes) of the revegetation study: Two seeding techniques (manual vs. hydro seeding) (blue box), three seed mixtures (hay threshing, regional seeds, commercial seeds) (green box) and different supporting measures (nurse species, hay mulch, fertilizer)(yellow box) for species establishment on embankments were tested from 2018 to 2020.

2.2. Chapter outline

The following section will give a brief overview of the research questions and hypotheses addressed in the respective chapters.

In **chapter 3**, we addressed the question how plant diversity and community composition change after vineyard abandonment. We expected abandoned vineyards to have a different vegetation than managed vineyards due to distinct disturbance intensities (no disturbance in fallows vs. intermediate - high disturbance in managed vineyards). Since extensive and environmentally friendly vegetation management in vineyard inter-rows (e.g. reduced tillage and mulching frequencies) increases plant and arthropod diversity (Hall et al. 2020; Winter et al. 2018) we assumed that distinct management in vineyard compartments (terraced vineyards: terrace inter-row, embankment; vertically oriented vineyards: vegetated inter-row, open inter-row) shapes different plant communities. We hypothesised that extensive vegetation management on embankments fosters high species diversity of herbaceous species, while in vegetated inter-rows of vertically oriented vineyards regular mulching and high vehicular disturbance lead to a higher grass cover (Dickson et al. 2008; York et al. 1997). As the management of open inter-rows of terraced and vertically oriented vineyards are similarly managed by regular tillage, we did not expect differences in plant communities but expected annual and ruderal species to prevail (Hall et al. 2020).

In **chapter 4**, we evaluated the importance of open habitat structures provided by vineyard management for grasshopper diversity, abundance, and community composition. We expected that shrub encroachment in abandoned vineyards decreases habitat quality for open-adapted grasshopper species (Schirmel et al. 2011; Marini et al. 2009), but hypothesised that Ensifera species that inhabit transitional habitats (Ortis et al. 2021) prevail in abandoned vineyards. For grasshoppers, spatial and structural heterogeneity through distinct vegetation structures provide habitats, distinct feeding opportunities and shelter against predators (Bonari et al. 2017; Gardiner et al. 2005). We, therefore, assumed that management in vineyard compartments (terraced vineyards: terrace inter-row, embankment; vertically oriented vineyards: vegetated inter-row, open inter-row) favours grasshopper species differently. We expected open-adapted grasshoppers to benefit from bare ground in open inter-rows of terraced and vertically oriented vineyards and hypothesised that extensively management vegetation of embankments with taller vegetation stands fosters grasshopper diversity in contrast to short and regularly mulched vegetation in vegetated inter-rows.

In **chapter 5**, the effects of the three different vineyard types and the surrounding landscape on wild bee diversity, abundance and community composition were investigated. Wild bees depend on floral resources and suitable nesting sites within species-specific flying distances as they return to their nests

after foraging (Greenleaf et al. 2007). In particular, we assumed that herbaceous vegetation and higher floral resource availability in managed vineyards and terraced vineyards benefit wild bee diversity and abundance. In addition, we expected that for nesting, ground-nesting bees benefit from bare ground in managed vineyards (Kratschmer et al. 2019) while above-ground-nesting bees benefit from woody structures of fallows at the local and landscape scale (Uzman et al. 2020). As the landscape context and the proportion of SNHs play an important role for wild bees (e.g. Warzecha et al. 2021), we assumed that the small-structured landscape of the study area contributes to a high species diversity.

In **chapter 6**, the effects of the three vineyard types and the surrounding landscape on spider diversity, abundance and community composition were evaluated. Distinct vegetation structures are known to determine spider community composition (Entling et al. 2007). Therefore, we assumed that herbaceous vegetation in managed vineyards and woody vegetation in abandoned vineyards shape different spider communities. We hypothesised that spider diversity benefits from extensive management on embankments while higher management intensities in vertically oriented vineyards favour the abundance of ruderal species. As spider species richness and abundance in vineyards are positively affected by SNHs, hedges and forests near vineyards (Kolb et al. 2020; Prieto-Benítez and Méndez 2011), we expected a positive effect of SNHs and forests in the surrounding landscape.

In **chapter 7**, the effects of different seeding techniques (manual vs. hydro-seeding), seed mixtures (hay threshing, regional and commercial mixture), and effects of nurse plants, hay mulch, and fertilizer on the establishment and maintenance of vegetation on three terraced vineyards were assessed. For winegrowers, a permanent vegetation cover on embankments is important to maintain stability and prevent soil erosion (Pijl et al. 2020; Rodrigo-Comino et al. 2019). For conservation objectives, embankments can act as valuable habitats with species-rich plant communities, but the local diaspore bank is usually species-poor and nearby seed-sources are missing. Hydro-seeding improves the adhesion of seeds on steep embankments and thus lowers the probability that seeds are washed or blown off in the early development stages (Elmarsdottir et al. 2003). We, therefore, expected that in comparison to manual seeding, hydro-seeding results in higher vegetation cover and establishment of target species. Due to the harsh environmental conditions on embankments, we hypothesised that locally adapted seed mixtures thrive better, provide a higher vegetation cover and have a lower failure risk. We further expected that hay mulch and nurse species improve microclimatic conditions and support the seedling establishment. We assumed that an initial fertilizer improves soil properties on embankments with sparse humus layers (Tormo et al. 2007) and thus enhances plant establishment.

3. Promoting plant diversity and habitat heterogeneity through vineyard terracing



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Parts of this chapter are currently under review

Author contribution:

VW: Conceptualization, Data curation, Data analysis, Investigation, Methodology, Visualization, Writing - original draft, Writing - review & editing. **KB:** Data curation, Investigation. **IL:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing - review & editing.

3.1 Abstract

Questions: Viticulture on steep slopes has shaped landscape and biodiversity in many regions, but insufficient profitability has led to management cessation and shrub encroachment. A solution to maintain cultivation economically viable could be vineyard terracing. We aimed to identify the potential of terracing to enhance plant diversity and habitat heterogeneity in vineyards, analyse the effects of management intensity on vineyard vegetation, and assess how plant communities change after vineyard abandonment.

Location: Wine-growing region of the Upper Middle Rhine Valley in Hesse (50.042342°N, 7.814533°E) and Rhineland-Palatinate (50.119139°N, 7.719275°E), Germany.

Methods: We recorded vascular plant species and local vineyard parameters in vertically oriented vineyards with vegetated and tilled open inter-rows, in terraced vineyards with tilled terrace inter-rows and extensively managed embankments and in vineyard fallows in a total of 45 study sites. We used plant species richness, Ellenberg indicator values and Grime's strategy types to describe how traits and ecological requirements respond to distinct vineyard management.

Results: Plant species richness and composition were determined by management-derived disturbance intensities. Extensively managed embankments had a distinct plant community, the highest plant species richness, more perennial and indicator species, and lower nitrogen indicator values compared to inter-rows. In contrast, highly disturbed open and terrace inter-rows revealed plant communities associated with annuals and ruderals, but species richness did not differ between terrace inter-rows and embankments. Plant communities of fallows were completely different with lower plant diversity.

Conclusions: Our results highlight the potential of terraced vineyards for plant diversity with nutrient-poor, extensively managed embankments providing conditions that have become rare in modern agricultural systems. A long environmental gradient from terrace inter-rows to embankments created habitat heterogeneity at a narrow space. In contrast, intensive inter-row management in vertically oriented vineyards hampers high plant diversity and abandonment fosters the spread of woody species at the expense of plant diversity.

3.2 Introduction

Traditional agricultural land use has shaped impressive cultural landscapes and ecosystems with high conservation value (Tieskens et al. 2017). In Europe, many species and species-rich ecosystems have evolved with traditional agricultural practices and thus rely on cultivation for their survival (Batáry et al. 2015; Sutcliffe et al. 2015). In recent decades, cultural landscapes have been seriously threatened by both large-scale intensification in highly productive areas and land abandonment on marginal and less suitable sites (Estel et al. 2015; Marini et al. 2011). The consequences of agricultural abandonment are context-dependent and thus controversially discussed. For one thing, in traditional farming systems, abandonment can lead to the loss of associated biodiversity (Queiroz et al. 2014) and then again can provide an opportunity for renaturation and ecosystem recovery (Pereira and Navarro 2015). However, according to the intermediate disturbance hypothesis (IDH), higher diversity levels are found at intermediate levels of disturbance while both poorly and highly disturbed systems harbour less biodiversity (Connell 1978; Grime 1973).

Traditional vine cultivation has been done in a mosaic of small vineyards, natural elements, field margins, stone walls, and hollow ways that provide valuable habitats for many thermophilous species and species-rich communities (Poschlod and Braun-Reichert 2017; Winkler et al. 2017). In Germany, cultivating vines on steep slopes has a long tradition and has shaped whole landscapes such as the Mosel or the Upper Middle Rhine Valley. Nevertheless, traditional cultivation on small dry-stone terraces has experienced severe management intensification and landscape simplification. During land consolidation measures in the 1960s vines were planted in a downhill direction (vertically oriented hereafter) to increase productivity, mechanization, and the area under cultivation. However, on steep slopes, mechanization is still difficult and complex leading to high manpower requirements and thus higher production costs (Strub et al. 2021). Therefore, the viticultural area on steep slopes has been declining substantially in the past decades due to insufficient profitability, thereby causing an increase in the area of fallow land (up to 39% in the Middle-Rhine Valley; 1987 – 2019) (Stoll and Schultz 2020). The progressive shrub encroachment threatens the flora and fauna associated with open habitats and extensive viticultural management as well as the cultural heritage.

One approach to keep management economically viable and thereby halt the decline of viticulture on steep slopes is the construction of modern, drivable vineyard terraces. Hillside parallel terraces help reduce production costs by favouring mechanization, accelerating manual work steps, and improving occupational safety (Strub and Loose 2021a). At the same time, a substantial area is composed of embankments that are left uncultivated and managed extensively (no fertilizer, no pesticide application, no vehicular disturbance) and therefore offer great potential to provide biodiversity refugia

3. Promoting plant diversity and habitat heterogeneity through vineyard terracing

(Wersebeckmann et al. 2023a; Košulič et al. 2014) within the agricultural system and might also contribute to habitat networking.

As viticulture is one of the most erosion-prone forms of land use (Garcia et al. 2018) maintaining vegetation cover in vineyard inter-rows (e.g. by sowing cover crops or natural vegetation) has become a common practice that has many advantages like erosion prevention, improved soil structure and fertility, weed suppression, and habitat provision for beneficial insects (Garcia et al. 2018; Guerra and Steenwerth 2012). However, inter-row vegetation is often managed intensively by regular tillage, mulching, or herbicide application to mitigate potential water and nutrient competition even though results are contrasting and many interacting factors like water regime, soil composition, management, age of vines, and (cover crop) species play a role (Giffard et al. 2022). Across studies, extensive and environmentally friendly vegetation management in vineyard inter-rows (e.g. reduced tillage and mulching frequencies) resulted in increased biodiversity and ecosystem service provision (reviewed by Winter et al. 2018) but might be gained at the expense of yields due to e.g. water stress and nutrient competition (Morlat and Jacquet 2003). Alternate management (i.e. one inter-row is kept bare while the other one is covered with vegetation) has been suggested to break the monotony in intensively managed vineyard landscapes (Brambilla and Gatti 2022) because within-field heterogeneity is increased, and distinct cultivation methods shaped differently composed plant communities and vegetation structures. Recently, more attention has been paid to enhancing the biodiversity potential of vineyards by diversifying plant communities and wild plant diversity in vineyard inter-rows (Blaise et al. 2022; Nascimbene et al. 2013). But frequent tillage and high vehicular disturbance due to high plant protection frequencies in viticulture adversely affect plant species richness because perennials and forbs are usually more sensitive to such disturbances and thus suffer greater losses (Dickson et al. 2008; York et al. 1997). The adaptation of biodiversity-friendly and low-intensity management practices might also involve supplementary costs and thus requires some willingness from the individual winegrowers (Garcia et al. 2018). Vineyard terraces might overcome these obstacles because management intensity and vehicular disturbance on embankments are inherently low. Thus, there is the potential to establish species-rich perennial plant communities on terrace embankments as observed on single sites (Richert et al. 2022) and at the same time maintain within-field heterogeneity through open terrace inter-rows.

In our study, we assessed the effects of differently managed vineyard types (vertically oriented vs. terraced vineyard) and vineyard abandonment on plant diversity. We hypothesized that low disturbance in fallows and high management-derived disturbance (tillage, mulching, driving) in vertically oriented vineyards reduces plant diversity while extensive management (intermediate disturbance) in terraced vineyards favours higher plant diversity levels (according to IDH). Additionally, we investigated how different management practices (tillage, vehicular disturbance, mulching,

extensive management) in vineyard compartments (open and vegetated inter-rows, embankments) affect within-field heterogeneity and shapes plant communities and plant diversity along a management-derived disturbance gradient in steep slope vineyards. The overall aim was to evaluate the potential of terraced vineyards for floristic enrichment and increasing habitat heterogeneity in steep slope vineyards.

3.3 Material and Methods

3.3.1 Study sites

The study was carried out in the wine-growing region of the Upper Middle Rhine Valley (UMRV) Germany, in Hesse (50.042342°N, 7.814533°E) and Rhineland-Palatinate (50.119139°N, 7.719275°E). The UMRV is a UNESCO World Heritage site and part of the 'Middle Rhine valley with side valleys Nahe and Mosel' a German biodiversity hotspot (Ackermann and Sachteleben 2012). As an ancient cultural landscape, it is characterized by a high diversity of habitats and xerothermophilic species of conservation concern (Ackermann and Sachteleben 2012). The landscape is small-structured with a mosaic of vineyard fallows, forest, and actively managed vineyards. The climate is sub Atlantic with an annual mean temperature of 11.6 °C and total annual precipitation of 554 mm (Lorch, 2015–2019, weather station Hochschule Geisenheim). Soils were clayey loam or loess soils, partially including limestone. Three sites had slate soils.

We studied three vineyard types of which two were actively managed (vertically oriented and terraced) while the other one was abandoned of management (fallow) (Figure 8). To account for structural differences within actively managed vineyards, we sampled vegetated and open inter-rows in vertically oriented vineyards and inter-rows and embankments in terraced vineyards (hereafter vineyard compartments) separately (Figure 8):

(i) **vertically oriented vineyards** have alternating management i.e., every second inter-row is kept with a perennial vegetation cover (vegetated inter-row hereafter) to maintain stability for tractor driving, while the other one is kept bare by tillage once or twice per season. To prevent competition for water and nutrients with vines, the vegetation of vegetated inter-rows is kept short by regular mulching. No cover crop mixtures were sown in inter-rows in the study year.

(ii) **terraced vineyards** comprise embankments that are permanently covered with perennial vegetation and mulched/mown once in summer, while terrace inter-rows are kept bare by regular tillage. No seed mixtures were sown in inter-rows or embankments in the study year. Terrace embankments were actively revegetated right after construction using commercial or regional seed mixtures whose exact composition is not known to us. The latest terraced vineyard was constructed in 2015.

3. Promoting plant diversity and habitat heterogeneity through vineyard terracing

(iii) **vineyard fallows** are not managed and abandoned for at least 10 years and were mostly overgrown with woody vegetation dominated by *Rubus fruticosus* agg., *Rosa canina* agg., *Prunus avium*, and *Crataegus laevigata*.

We arranged vineyard types in triplets with each triplet including a vertically oriented vineyard, a terraced vineyard, and a vineyard fallow (Figure 8). We studied a total of 15 triplets (45 sites) that were managed by 14 different winegrowers according to the standards of integrated pest management (EU Directive 2009/128/EC). Therefore, grape variety, age of the vines, and size of the vineyard area differed between sites. Study sites within a triplet were arranged close to each other to ensure similar environmental conditions. The inclination ranged from 17° to 42°.

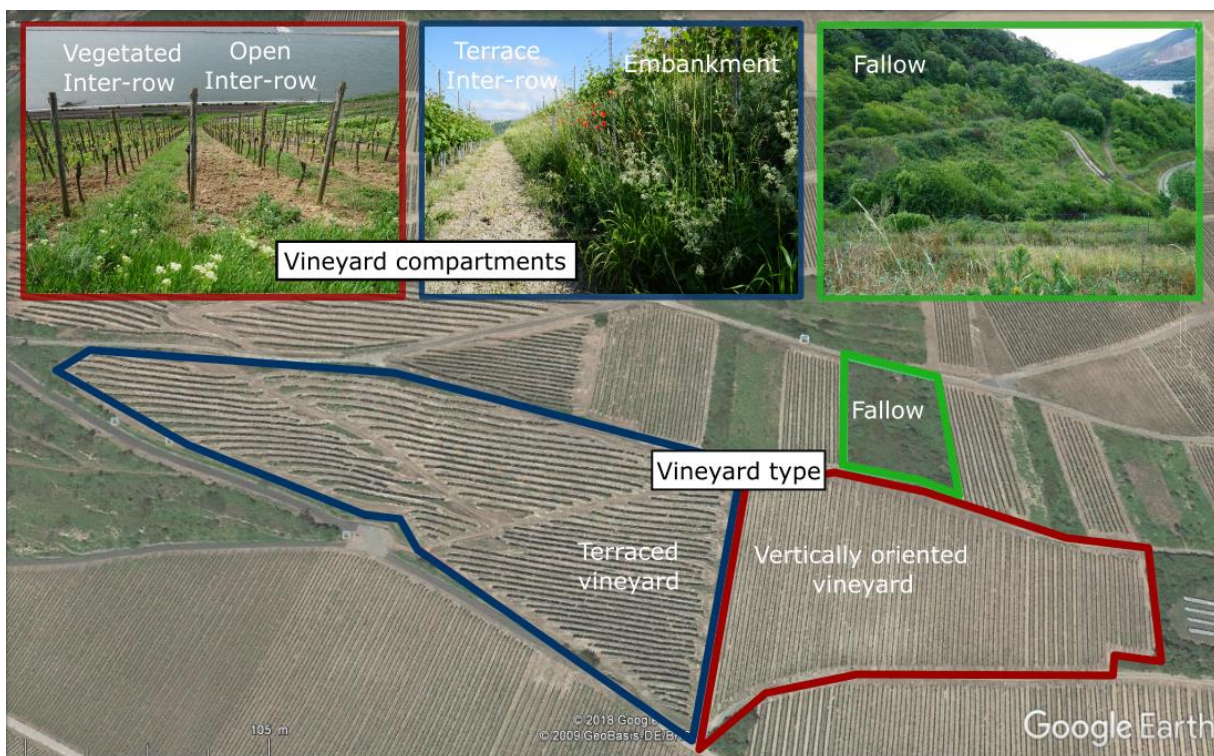


Figure 8: Three vineyard types were studied: vertically oriented vineyards that received alternating management with one open inter-row being regularly tilled and the other one being permanently covered with vegetation (vegetated inter-row), terraced vineyards with regularly tilled terrace inter-rows and extensively managed vegetation on embankments and vineyard fallows that were not managed and abandoned for at least 10 years.

3.3.2 Vegetation assessment

Vegetation surveys were carried out in 2019 in two sampling rounds in March and June-July. For each sampling round, two pairs of vegetated and open inter-rows were selected in the centre of each vertically oriented vineyard and two pairs of embankments and terrace inter-rows were selected in the centre of each terraced vineyard. The plant community was assessed in rectangles of 1 x 6 m in each selected inter-row and embankment (vineyard compartments) respectively, resulting in four quadrats per vineyard and sampling round. As fallows were difficult to assess due to dense shrub, we used one plot of 4 x 6 m for vegetation surveying. Within each plot, we identified all vascular plants and estimated

their respective ground cover according to Londo (Londo 1976). We additionally estimated the percentage cover of total vegetation, bare ground, litter, shrubs, and trees. Species were identified using the reference works from Ritz et al. (2021) and Eggenberg and Möhl (2020). All cultivars of *F. rubra* were summarised as *F. rubra* since they could not be distinguished in the field. Species that could not be reliably identified were excluded from species-level analysis (5 individuals). Nomenclature follows Buttler et al. (2018).

3.3.3 Data analysis

All statistical analyses were carried out using the R environment (R Core Team 2020). Figures were created with `ggplot2` (Wickham 2016). For statistical analysis, Londo cover-abundance values were transformed into mean values according to Leyer and Wesche (2007), and mean values for percentage cover of total vegetation, bare ground, litter, shrub, and tree cover were calculated and averaged over the two sampling rounds. To determine the total cover of herbaceous vegetation and grasses per plot, we added up all transformed cover values of the respective grass and herbaceous species.

To describe site-specific factors, we calculated Ellenberg indicator values for nitrogen, temperature, light, moisture, and reaction for each vineyard compartment. Only presence-absence data of species abundance were used to compute mean indicator values (i.e. resulting in unweighted means) to avoid overestimation of rampantly growing species (Diekmann 2003). Species without existing Ellenberg values were excluded from the analyses. To account for distinct management-related disturbance intensities, we implemented a disturbance gradient ranging from high disturbance (1) in open and terrace inter-rows, to intermediate disturbance in vegetated inter-rows (2) and embankments (3) to low disturbance (4) in fallows. To describe the ecological traits of plant species, we calculated CSR strategy types according to Grime (2002) for each site. We used a numerical implementation to handle the strategy types mathematically and translated the three categories (CSR) into values ranging from 0-3 for each of the three strategy dimensions (competitiveness, stress tolerance, and ruderality). The three scores of each species sum up to three and each score corresponds to the number of the respective letter in the strategy category. We calculated mean values for each strategy type for each site based on presence-absence data. We obtained data from the flora web database (Federal Office for Nature Conservation 2023) to describe differences between life forms (annual, biennial, perennial) according to Klotz et al. (2002). Indicator species for each compartment were generated using the `IndVal` procedure of Dufrêne and Legendre (1997), which combines species abundance with its relative frequency of occurrence within the different vineyard types (function “`multipatt`” in the R package `indicpecies` (Cáceres and Legendre 2009)). P-values were obtained using a permutation test with 9999 permutations.

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3.3.3.1 Multivariate analysis

To analyse differences in plant species composition in relation to vineyard types we conducted a detrended correspondence analysis (DCA) since the length of gradient of 1st DCA-axis (5.45) suggested a unimodal relationship (package: *vegan*, function: *decorana* (Oksanen et al. 2020)). To reduce the influence of dominant species, we $\log_{10}(x + 1)$ transformed the community data and excluded species with less than three occurrences from the analysis (96 species remain). To identify potential underlying factors, percentage covers, Ellenberg indicator values, strategy types, life forms and the disturbance gradient were correlated with the ordination axes using the function *envfit* (package: *vegan*), and the significant correlations were added post-hoc to the ordination graph. All variables were standardized to zero mean and unit variance before the analysis (function “*scale*”, package: *vegan*).

3.3.3.2 Univariate Analysis

We choose (generalized) linear mixed effect models (GLMMs) for analysis. Data exploration was conducted according to Zuur et al. (2010). To analyse differences between vineyard types and compartments and local vegetation parameters, Ellenberg indicator values, strategy types, life forms, and species richness we fitted (G)LMMs with vineyard compartment as fixed and vineyard triplet (factor with 15 levels) as a random effect (package: *glmmTMB* (Brooks et al. 2017)). Depending on the distribution of the response variable and residuals, models were fitted with Gaussian family and Poisson family for count data (species richness). Post-hoc-pairwise comparisons (Tukey method) were performed using the *emmeans* package (Lenth 2020).

3.4 Results

In total, we recorded 176 vascular plant species, 119 in vertically oriented vineyards, 151 in terraced vineyards, and 68 in fallows (Table A. 1). We recorded three species of conservation concern (Table A. 1).

3.4.1 Differences in plant species composition

Plant communities showed a clustering along a disturbance gradient from a high mechanical disturbance in open and terrace inter-rows to an intermediate disturbance in vegetated inter-rows and embankments to a low disturbance in fallows (Figure 9). While fallows were clearly separated from terrace, open and vegetated inter-rows, embankments were in between. Fallows were positively correlated with higher shrub and tree cover, competitive species, and indicator value for reaction while embankments were more closely associated with herbaceous cover and indicator value for temperature. For all inter-rows and terrace inter-rows in particular, there was a pronounced relationship with high disturbance intensity, ruderal and annual species, grass cover and indicator value for light (Table A. 2), while open and vegetated inter-rows were associated with bare ground, biennial species and indicator value for nitrogen and moisture.

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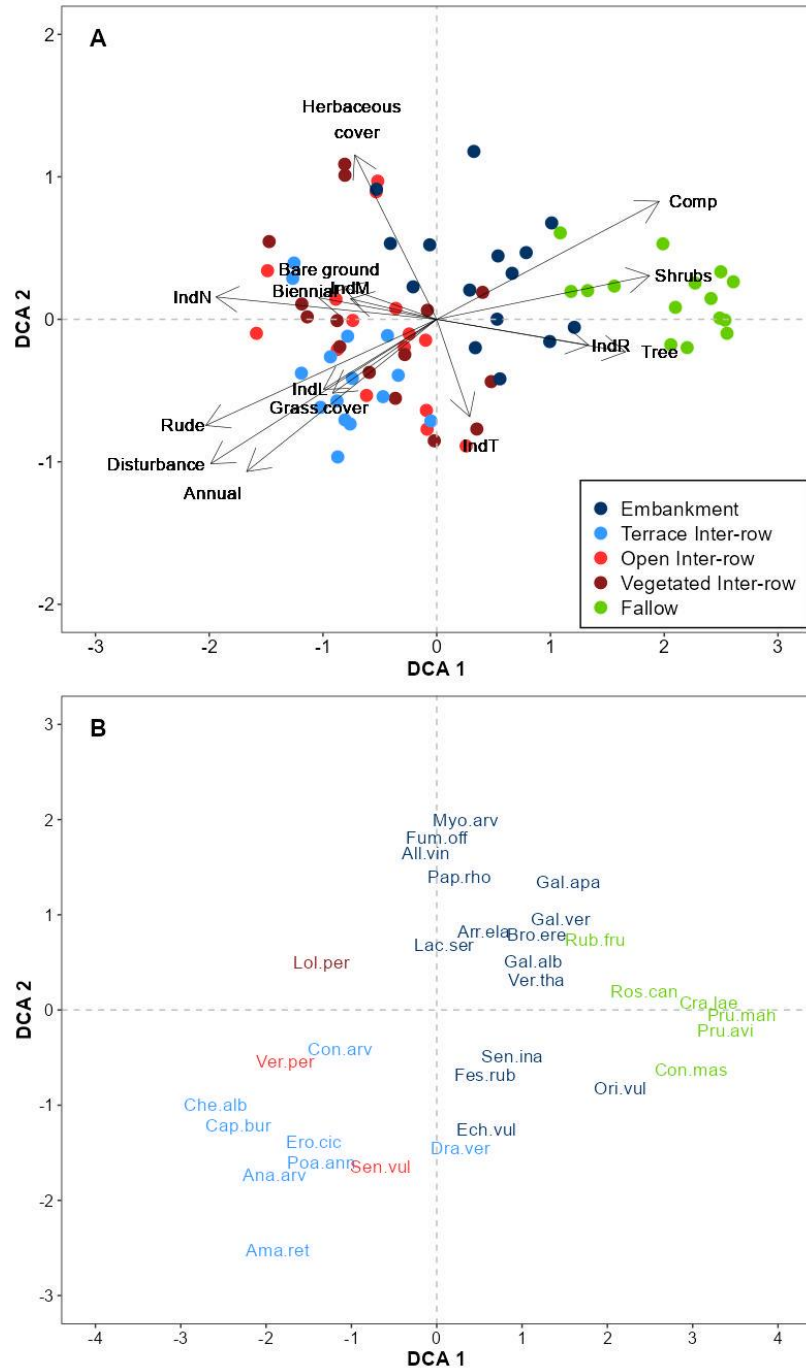


Figure 9: DCA results for plant species composition of vineyard compartments (length of 1st DCA-axis: 5.45, 2nd DCA-axis: 2.93). Dots show scores for embankment (dark blue), terrace inter-row (light blue), open inter-row (light red) and vegetated inter-row (dark red). Environmental and indicator variables that were significantly related to the DCA axes ($p < 0.05$, 9999 permutations) were included post-hoc by projection. To aid visualization, vineyard compartments (A) and indicator species (B) of terrace embankments (dark blue), terrace inter-rows (light blue), vegetated inter-rows (dark red), and open inter-rows (light red) are shown as separate graphs. Species abbreviations: All.vin: *Allium vineale*, Ama.ret: *Amaranthus retroflexus*, Ana.arv: *Anagallis arvensis*, Arr.ela: *Arrhenatherum elatius*, Bro.ere: *Bromus erectus*, Cap.bur: *Capsella bursa-pastoris*, Che.alb: *Chenopodium album*, Con.arv: *Convolvulus arvensis*, Cor.mas: *Cornus mas*, Dra.ver: *Draba verna*, Ech.vul: *Echium vulgare*, Ero.cic: *Erodium cicutarium*, Fes.rub: *Festuca rubra*, Fum.off: *Fumaria officinalis*, Gal.alb: *Galium album*, Gal.apa: *Galium aparine*, Gal.ver: *Galium verum*, Lac.ser: *Lactuca serriola*, Lol.per: *Lolium perenne*, Myo.arv: *Myosotis arvensis*, Ori.vul: *Origanum vulgare*, Pap.rho: *Papaver rhoeas*, Poa.ann: *Poa annua*, Pru.avi: *Prunus avium*, Pru.mah: *Prunus mahaleb*, Ros.can: *Rosa canina* agg., Rub.fru: *Rubus fruticosus* agg., Sen.ina: *Senecio inaequidens*, Sen.vul: *Senecio vulgaris*, Tra.dub: *Tragopogon dubius*, Ver.tha: *Verbascum thapsus*, Ver.per: *Veronica persica*.

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3.4.2 Differences between vineyard types and compartments

Species richness differed significantly between vineyard types (Figure 10 A) and vineyard compartments (Figure 10 B). In vineyard types, species richness was highest in terraced vineyards and lowest for fallows with vertically oriented vineyards in between. In vineyard compartments, plant species richness was higher on embankments compared to vegetated and open inter-rows and fallows but did not differ significantly from terrace inter-rows. Vegetation cover was significantly lower in open inter-rows than in vegetated inter-rows while there was no difference to embankments, terrace inter-rows and fallows (Table 1). Bare ground cover was significantly higher for terrace inter-rows than for vegetated inter-rows, embankments and fallows while there was no difference compared to open inter-rows (Table 1). Shrub cover only occurred on embankments and fallows and was significantly higher for the latter. Grass cover was significantly highest in vegetated inter-rows compared to terrace inter-rows and fallows, while the herbaceous cover was highest on embankments and lowest in fallows. Analysis of life forms revealed a significantly higher number of perennial species on embankments compared to all other inter-rows and fallows while the number of biennial species did not differ between embankments, open and terrace inter-rows, but was lower for vegetated inter-rows and fallows. Annual species had the highest numbers in terrace inter-rows but did not differ from embankments and open inter-rows. For fallows, the number of annual species was the lowest (Table 1).

Table 1: Effects of vineyard types on local vegetation parameters and number of annual, biennial, and perennial species (N = 15). Different letters show significant differences within the respective vineyard types ($p < 0.05$).

Variable	Vertically oriented		Terrace	Fallow	
	Vegetated Inter-row	Open Inter-row	Embankment	Terrace Inter-row	
Vegetation cover [%]	59.43 ^b ± 7.75	35.91 ^a ± 4.99	52.92 ^{ab} ± 3.33	43.15 ^{ab} ± 3.85	51.00 ^{ab} ± .34
Bare ground cover [%]	25.96 ^a ± 5.29	51.96 ^{bc} ± 6.87	33.42 ^{ab} ± 3.74	56.58 ± 7.52 ^c	20.00 ± 3.98 ^a
Litter cover [%] ⁺	12.94 ± 2.56	8.27 ± 0.96	15.33 ± 1.85	11.67 ± 2.55	10.13 ± 2.35
Shrub cover [%]	0.00 ^a ± 0.00	0.00 ^a ± 0.00	0.91 ^a ± 0.37	0.00 ^a ± 0.00	50.33 ^b ± 7.13
Tree cover [%]	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	18.67 ± 4.46
Herbaceous cover [Londo]	68.93 ^b ± 10.45	65.53 ^b ± 10.35	108.80 ^a ± 9.15	87.60 ^{ab} ± 0.61	3.40 ^c ± 1.53
Grass cover [Londo]	68.73 ^a ± 11.81	34.80 ^{ab} ± 9.82	62.47 ^{ab} ± 8.51	31.73 ^b ± 6.64	30.60 ^c ± 7.78
Nr. of annual species	10.87 ^b ± 1.03	12.93 ^{ab} ± 1.16	12.07 ^{ab} ± 1.26	15.07 ^a ± 0.71	1.13 ^c ± 0.31
Nr. of biennial species	3.80 ^b ± 0.44	4.07 ^{ab} ± 0.44	5.27 ^a ± 0.41	4.47 ^{ab} ± 0.46	0.60 ^c ± 0.29
Nr. of perennial species	12.00 ^b ± 1.18	10.07 ^b ± 1.18	17.20 ^a ± 1.12	11.80 ^b ± 1.17	9.47 ^b ± 0.10

+ square-root transformed data were used for testing

Embankments had lower Ellenberg nitrogen values compared to all inter-rows while fallows had the lowest nitrogen indicator values (Figure 10 C). Ellenberg indicator values for reaction were significantly lower in terrace inter-rows compared to fallows and all other inter-rows (Figure 10 D). For the indicator value light, fallows had significantly lower values than all vineyard inter-rows and embankments (Figure

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10 E) while there were no differences for Ellenberg indicator values of temperature and moisture (Figure A 1. A-B). Regarding plant strategies, competitive species were most abundant in fallows and had the lowest abundances in open and terraced inter-rows (Figure 10 F), while there were no differences for stress-tolerant species (Figure 10 G). Ruderal species were most abundant in terrace and open inter-rows and had low abundances in fallows (Figure 10 H).

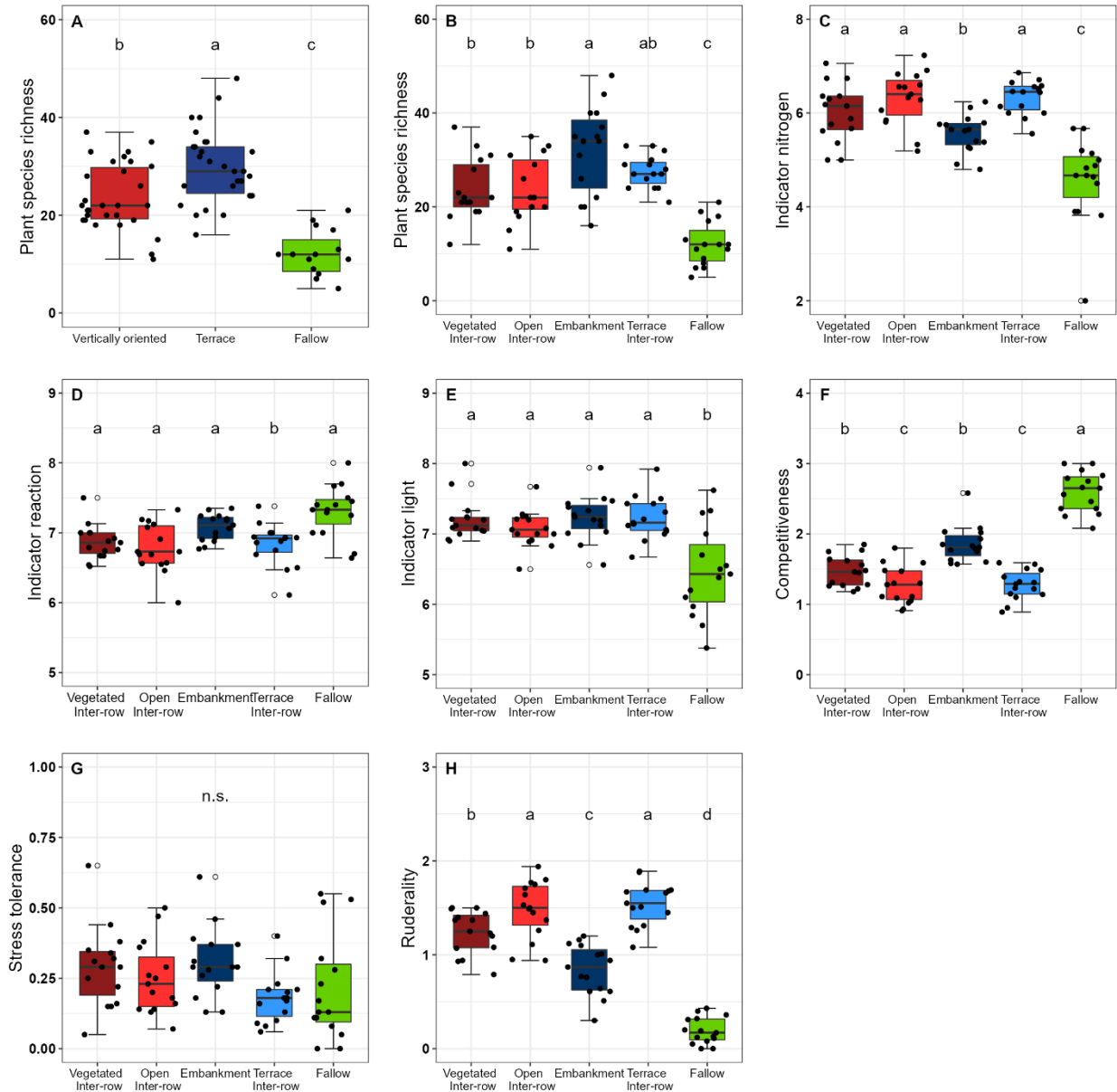


Figure 10: Differences in species richness of plants between vineyard types (A) and vineyard compartments (B), and differences between mean Ellenberg indicator values for nitrogen (C) reaction (D), light (E), and CSR strategies competitiveness (F), stress tolerance (G), and ruderality (H) between vineyard compartments analyzed using (G)LMMs. Each data point represents the number of species (A, B) or mean value per site (C-H) for the respective vineyard compartments (N = 15). Different letters indicate significant differences between vineyard compartments ($p < 0.05$).

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Indicator species analysis revealed 31 plant species that were significantly associated with one vineyard compartment (Table 2). Compartments of terraced vineyards revealed many indicator species of which most species were associated with embankments (15), followed by terrace inter-rows (8) while compartments of vertically oriented vineyards had very few indicator species.

Table 2: Indicator plant species and the respective number of records for the five vineyard compartments (N = 15). Species significantly associated with one vineyard compartment are printed in bold. Respective p-values are given ($p < 0.05$).

Indicator species	Vertically oriented		Terrace		Fallow	p-value
	Vegetated Inter-row	Open Inter-row	Embankment	Inter-row		
1 <i>Allium vineale</i>	0	0	7	1	0	0.0011
2 <i>Amaranthus retroflexus</i>	1	5	0	17	0	0.0001
3 <i>Anagallis arvensis</i>	4	6	1	8	0	0.0085
4 <i>Arrhenatherum elatius</i>	19	16	39	14	5	0.0016
5 <i>Bromus erectus</i>	0	0	15	1	0	0.0003
6 <i>Capsella bursa-pastoris</i>	1	6	1	10	0	0.0044
7 <i>Chenopodium album</i>	2	6	2	15	0	0.0147
8 <i>Convolvulus arvensis</i>	11	11	13	19	0	0.0050
9 <i>Cornus mas</i>	0	0	2	0	12	0.0001
10 <i>Crataegus laevigata</i>	0	0	2	0	14	0.0001
11 <i>Draba verna</i>	4	8	8	11	1	0.0200
12 <i>Echium vulgare</i>	3	1	16	9	2	0.0171
13 <i>Erodium cicutarium</i>	12	9	4	28	0	0.0002
14 <i>Festuca rubra agg.</i>	12	4	27	7	3	0.0048
15 <i>Fumaria officinalis</i>	2	4	8	0	1	0.0079
16 <i>Galium album</i>	16	7	39	16	12	0.0001
17 <i>Galium aparine</i>	0	3	14	0	4	0.0003
18 <i>Galium verum</i>	3	0	17	1	5	0.0002
19 <i>Lactuca serriola</i>	5	11	31	13	0	0.0002
20 <i>Lolium perenne</i>	27	13	4	20	0	0.0001
21 <i>Myosotis arvensis</i>	0	0	5	0	0	0.0052
22 <i>Origanum vulgare</i>	1	1	7	1	4	0.0377
23 <i>Papaver rhoeas</i>	2	2	12	3	0	0.0001
24 <i>Poa annua</i>	4	5	1	27	0	0.0002
25 <i>Prunus avium</i>	0	0	1	0	18	0.0001
26 <i>Prunus mahaleb</i>	0	0	0	0	16	0.0001
27 <i>Robinia pseudoacacia</i>	0	0	0	0	4	0.0327
28 <i>Rosa canina agg.</i>	5	3	13	0	29	0.0001
29 <i>Rubus fruticosus agg.</i>	7	7	37	7	29	0.0001
30 <i>Senecio inaequidens</i>	0	2	8	2	0	0.0010
31 <i>Senecio vulgaris</i>	14	19	4	14	0	0.0430
32 <i>Verbascum thapsus agg.</i>	1	1	6	0	2	0.0314
33 <i>Veronica persica</i>	19	27	7	20	0	0.0001
Nr. of indicator species	1	2	15	8	7	

3.5 Discussion

In the present study, the highest diversity levels were found on vineyard terrace embankments with intermediate disturbance intensities. Our results indicate that terrace embankments with extensive management and lower nutrient levels have the potential to establish species-rich, perennial plant communities. In contrast, plant functional traits like ruderality and annual species were related to tillage management in open and terraced inter-rows while vehicular disturbance and mulching in vegetated inter-rows fostered a higher grass cover. The plant community of abandoned vineyards completely differed from those in actively managed vineyards, underlining the importance of viticulture to maintaining the characteristic vegetation of these cultural landscapes.

3.5.1 Effects of vineyard types on plant diversity

Disturbance intensity and vegetation management determined plant species richness in vineyard types. Both, higher disturbance in vertically oriented vineyards and low disturbance in abandoned vineyards resulted in a lower plant species richness in comparison to terraced vineyards with intermediate disturbances. Fallows had the lowest species richness and revealed little significance for plant diversity but provide other valuable ecological functions instead as woody elements in vineyard landscapes have high conservation value for other groups like wild bees (Wersebeckmann et al. 2023b; Uzman et al. 2020) or birds (Assandri et al. 2016; Pithon et al. 2016). The high species richness in terraced vineyards is not only attributable to an intermediate disturbance on embankments but to a long environmental gradient driven by different management, nutrient levels and disturbance intensities in terrace inter-rows and embankment that create distinct habitat conditions at a very narrow space.

3.5.2 Management-related differences in plant species composition and diversity

Distinct management practices and disturbance intensities in vineyard compartments shape different botanical compositions (Gut 1997) with high management intensities resulting in lower species richness, functional diversity, and vegetation cover (Hall et al. 2020; Paiola et al. 2020). Analysis of plant species composition revealed differences along a gradient from a high mechanical disturbance in open, terrace and vegetated inter-rows to low disturbance in fallows with intermediate disturbance on terrace embankments in between. In open and terrace inter-rows regular tillage fostered the dominance of annuals which can germinate and establish throughout the vegetation period (Hall et al. 2020) and a higher mean number of ruderal strategists compared to vegetated inter-rows. Particularly striking was that at the community level and when looking at strategy types terrace inter-rows revealed plant species more similar to those of open inter-rows, while species richness and herbaceous cover did not significantly differ from extensively managed embankments. One explanation could be the transfer of seeds from embankments that slide down during mowing or mulching. This is indicated by individual species (e.g., *Echium vulgare* or *Tanacetum vulgare*) in terrace inter-rows that frequently

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occurred on embankments but which we would not expect to establish in frequently tilled inter-rows. Further, in terrace inter-rows, early blossoming plants like *Draba verna* or *Capsella-bursa pastoris* were abundant before first soil tillage in spring and contributed to overall species richness in terrace inter-rows. Even though management in open and terrace inter-rows is similar, different inclinations and row orientation may have influenced plant species composition as terrace inter-rows are more shaded by vine plants than open inter-rows. A change in row orientation under steep slope conditions has been shown to modify light and microclimatic conditions in the vineyard and affected grapevine fruit parameters within the same study setup (Strack and Stoll 2021). Further, the inclination of the inter-row (terrace inter-row: flat, open inter-row: steep) alters the solar energy input and increases with increasing slope (Hoppmann et al. 2017). Consequently, differences in species composition between open and terrace inter-rows could be related to differences in microclimatic conditions and light interception but further investigation into this is needed.

In vegetated inter-rows disturbance is lower compared to open and terrace inter-rows and Hall et al. (2020) recorded higher plant diversity with more perennials in vegetated compared to open inter-rows across four European wine-growing regions. In general, the potential to enhance plant diversity is higher in vegetated inter-rows with moderate disturbance but our results did not reveal a higher plant diversity. Instead, we found a higher grass cover which is likely because graminoids show higher resistance and resilience to vehicular and trampling disturbance while broad-leaved herbs are more sensitive (Dickson et al. 2008; York et al. 1997). In addition, frequent mulching without biomass removal can substantially increase nutrient availability resulting from decomposition (Gaisler et al. 2013) and competition for light which leads to plant diversity decline in favour of grasses (Gillespie et al. 2022; Caboň et al. 2021). Thus, mulching combined with vehicular disturbance decreased the abundance of perennial herbs in our study system and leads to rather short swards (Gut 1997).

Extensive management on terrace embankments led to the highest plant diversity with both high grass and herbaceous cover as well as high numbers of annuals, biennials, and perennials. Embankments had the most indicator species including characteristic vineyard species (*Allium vineale*) and light-demanding species (*Echium vulgare*). Interestingly, we found lower indicator nitrogen values on embankments compared to all inter-rows and fallows which can be partly explained by mineralization processes after soil tillage and fertilizer applications in inter-rows, even if application rates in viticulture are usually low (Guerra and Steenwerth 2012). In addition, fine sediments and thus nutrients are more likely to be washed from steep embankments into terrace inter-rows (personal observation V.W.). These findings are particularly interesting for developing species-rich plant communities on embankments because nutrient-poor sites have become rare within agricultural systems. Higher nitrogen contents in the soil decrease plant diversity, alter competitive interactions and result in

increased plant growth and hence competition for light which in turn leads to changes in species composition in favour of grasses (Stevens et al. 2004; Bobbink et al. 1998). Grasses are assumed to exploit available N more rapidly and thus suppress forb species of smaller stature by a faster growth (Duprè et al. 2010).

3.5.3 Increasing the potential of terrace embankments

Especially on steep slopes with warm and dry climates, vineyards can be of high conservation value for xerothermic and rare species and topographic factors such as slope, aspect and shallow soils with low water and nutrient availability can promote high plant species richness (Nascimbene et al. 2013). Looking at embankments, preconditions for high plant species richness (extensive management, lower nitrogen availability) are favourable. However, despite the higher plant species richness, we found very few rare and threatened species and typical grassland species like *Leucanthemum ircutianum* or *Knautia arvensis* had only low abundances on embankments. This might be explained twofold: for one thing, biomass is usually not removed after mulching/mowing which leads to a litter cover and thus increased competition for light (Hautier et al. 2009). Light has a major influence on germination and establishment and thus on species composition (Jensen and Gutekunst 2003). Consequently, the accumulation of biomass favours fast-growing grasses over the more conservation-relevant target species in the long term. Secondly, the local diaspore bank in vineyards can be poor in species after decades of intensive viticultural management and nearby seed sources are often missing (Wersebeckmann et al. 2022).

Increasing plant biodiversity on terrace embankments should start with the implementation of more targeted cutting regimes that include biomass removal, cutting date, and frequencies. To favour herbaceous species and weaken expansive perennial tall grass species (e.g. *Arrhenatherum elatius*) adjusting the time and height of mowing can be a useful tool (Wilson and Clark 2001). Mowing grasses at the time of flowering, when carbohydrate concentrations in above-ground tissue are highest, and choosing a proper height for mowing that targets taller grass species while shorter herbs remain undamaged is most effective (Hulme et al. 1999; Becker and Fawcett 1998) and could also help to reduce the undesirable expansion of woody species (e.g. *Rosa canina* agg.) (Dostálek and Frantík 2012). A second cut could be reasonable in high precipitation years with higher biomass production (Moog et al. 2002). There always is a conflict between the necessity to mow to maintain plant diversity and the detrimental effect of mowing on invertebrates (Marini et al. 2009). These effects could be mitigated by leaving temporarily uncut vegetation patches that provide refuge in the close surrounding (Buri et al. 2013; Humbert et al. 2012). To overcome seed and dispersal limitations reintroduction of target species is necessary (Rudolph et al. 2017) but turned out to be difficult when a vegetation cover is already established on embankments (data not shown, Bachelor thesis Dries 2020). In contrast, revegetating

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newly build terrace embankments with regional seed mixtures has been a promising approach (Wersebeckmann et al. 2022).

3.6 Conclusion

Terraced vineyards revealed the highest plant species richness due to the interplay of nutrient-poor and moderately disturbed habitat conditions on embankments and a long environmental gradient from terraced inter-rows to embankments that created distinct habitat conditions at a very narrow space. Our results highlight the potential of terraced vineyards to maintain characteristic vegetation and nutrient-poor-herbaceous habitats within viticultural management systems.

4. Orthopteran diversity in steep slope vineyards: the role of vineyard type and vegetation management



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Author contribution:

VW: Conceptualization, Data curation, Data analysis, Investigation, Methodology, Visualization, Writing - original draft, Writing - review & editing. **CB:** Conceptualization, Data curation, Data analysis, Investigation, writing—original draft preparation. **KM:** Methodology, Supervision, Writing - review & editing. **IL:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing - review & editing.

4. Orthopteran diversity in steep slope vineyards: the role of vineyard type and vegetation management

4.1 Abstract

The abandonment of traditional agricultural practices and subsequent succession are major threats to many open-adapted species and species-rich ecosystems. Viticulture on steep slopes has recently suffered from strong declines due to insufficient profitability, thus increasing the area of fallow land considerably. Changing cultivation systems from vertically oriented to modern vineyard terraces offers an opportunity to maintain management economically viable and thus reduces further abandonment. Hillside parallel terraces favour mechanization, and their embankments offer large undisturbed areas that could provide valuable habitats. We investigated the effects of vineyard abandonment, different vineyard management types (vertically oriented vs. terraced), and local parameters on Orthoptera diversity in 45 study sites along the Upper Middle Rhine Valley in Germany. Our results show that woody structures and vineyard abandonment reduced Orthoptera diversity at the local and landscape scale due to decreased habitat quality, especially for open-adapted species. In contrast, open inter-rows of actively managed vineyard types supported heat-adapted Caelifera species. On terrace embankments, extensive management and taller vegetation benefited Ensifera species, while short and mulched vegetation in vertically oriented vineyards favoured the dominance of one single Caelifera species. Our results highlight the significance of maintaining viticultural management on steep slopes for the preservation of both open-adapted Orthoptera species and the cultural landscape.

4.2 Introduction

Insect populations are declining at unprecedented rates (Cardoso et al. 2020; Harvey et al. 2020; Thomas et al. 2019). The causes are much debated, but almost certainly include agricultural intensification, land-use change, and the abandonment of traditional agricultural practices (Habel et al. 2019; Sánchez-Bayo and Wyckhuys 2019). Since the second half of the 20th century in Europe, land-use intensification has been a major driver of the loss of farmland biodiversity (Sutcliffe et al. 2015; Kleijn et al. 2009). However, when intensification is not profitable, fields and meadows, especially on difficult-to-access hilly sites, are abandoned and thereby lose much of their ecological value for species adapted to open habitats by natural afforestation (Marini et al. 2011; Plieninger et al. 2006).

In Germany, viticulture on steep slopes has a long tradition and has shaped entire cultural landscapes such as the Mosel or the Upper Middle Rhine Valley. Traditionally, vines were cultivated on small terraces made of dry-stone walls intermingled with natural elements like hedges, trees, and clearance cairns (Treiling 2008). This traditional land-use practice created high structural diversity and provided habitats for many xerothermophilic and nowadays often endangered species, such as the Western green lizard (*Lacerta bilineata*), Red-winged grasshopper (*Oedipoda germanica*), and Scarce swallowtail (*Iphioides podalirius*) (Veith et al. 2012; Treiling 2008). During land consolidation measures in the 1960s, small vineyard terraces were merged into large vineyard sites with down-hill-oriented rows (vertically planted vineyards hereafter, see Figure 11 (a)) to increase productivity, mechanization, and the area under cultivation (Strub et al. 2021). However, the cultivation of vines on steep slopes still requires substantial manual work and due to increased labour costs, vertically planted vineyards have become unprofitable (Strub and Loose 2021b). Consequently, steep slope vineyards have increasingly been abandoned in the past decades (up to 39% in the Middle-Rhine Valley; 1987 – 2019) (Stoll and Schultz 2020). Of the former 2,500 hectares in 1909, only about 450 hectares remain in the Middle Rhine Valley today (State Statistical Office of Rhineland-Palatinate 2021). The progressive expansion of fallow land and ongoing succession threatens the flora and fauna adapted to traditional viticultural management and limits the livelihood opportunities of the local population.

One approach to halting viticultural decline on steep slopes is modern vineyard terracing (see Figure 11(b)). Here, hillside parallel inter-rows favour mechanization, facilitate management and manual work steps, and thus reduce costs considerably (Strub and Loose 2021a). At the same time, terrace embankments offer large uncropped areas between the vines that can provide valuable habitats (Wersebeckmann et al. 2021).

Orthopterans are important components of grassland invertebrate assemblages in European agricultural ecosystems (Báldi and Kisbenedek 1997), particularly due to their significant role as both

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herbivores and prey for a wide range of taxa such as birds (Badenhausser and Cordeau 2012; Gardiner and Dover 2008; Vickery et al. 2001). Their high sensitivity and rapid response to environmental changes also make them suitable indicator organisms (Fartmann et al. 2012; Báldi and Kisbenedek 1997). The impacts of land use change and succession on Orthoptera in European landscapes are well described for open habitats like grasslands and heathlands (Weiss et al. 2013; Schirmel et al. 2011; Marini et al. 2008) but there is a lack of studies addressing these impacts in vineyards. Moreover, the value of steep slope viticulture for Orthoptera diversity and the effects of various management systems in steep slope viticulture on Orthoptera have not yet been studied.

This study aims to assess the value of steep slope viticulture for Orthoptera diversity and to evaluate the impacts of ongoing succession as a consequence of vineyard abandonment. In this study, we compared Orthoptera diversity among abandoned vineyards (fallows) and two different vineyard management types (vertically oriented vs. terraced) in a viticultural landscape in Germany and addressed the following research questions: (i) How do Orthoptera species richness, density, and species composition shift across abandoned and managed vineyard types? (ii) How do management-related structures within vineyards affect species richness, density, and species composition?

4.3 Materials and Methods

4.3.1 Study area and sampling design

The study area is situated in the winegrowing region of the Upper Middle Rhine Valley (UMRV) in Rhineland-Palatinate (50.119139°N, 7.719275°E) and Hesse (50.042342°N, 7.814533°E), Germany (Figure 12). The climate is sub-Atlantic with an annual mean temperature of 12.4 °C and average annual precipitation of 462 mm in the study year (2020) (Hochschule Geisenheim University 2020). Soils were clayey loam or loess soils, partially including limestone. Three sites had slate soils. We studied three vineyard types (Figure 11):

(i) **vertically oriented vineyards** received an alternating tillage treatment, i.e., every second inter-row was kept open by regular tillage while the other inter-row was permanently covered with grassy vegetation dominated by *Lolium perenne*. To prevent competition for water and nutrients with vines, inter-row vegetation was kept short by regular mulching.

(ii) **terraced vineyards** received a regular tillage treatment in inter-rows, while terrace embankments were permanently covered with grassy and herbaceous vegetation such as *Arrhenaterum elatius*, *Bromus erectus*, *Galium album*, and *Isatis tinctoria*. Embankment vegetation was extensively managed and mulched/mown once in summer.

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(iii) **vineyard fallows** were abandoned for at least 10 years and were mostly overgrown with woody vegetation dominated by *Rubus fruticosus* agg., *Rosa canina* agg., *Prunus avium*, and *Crataegus laevigata*.

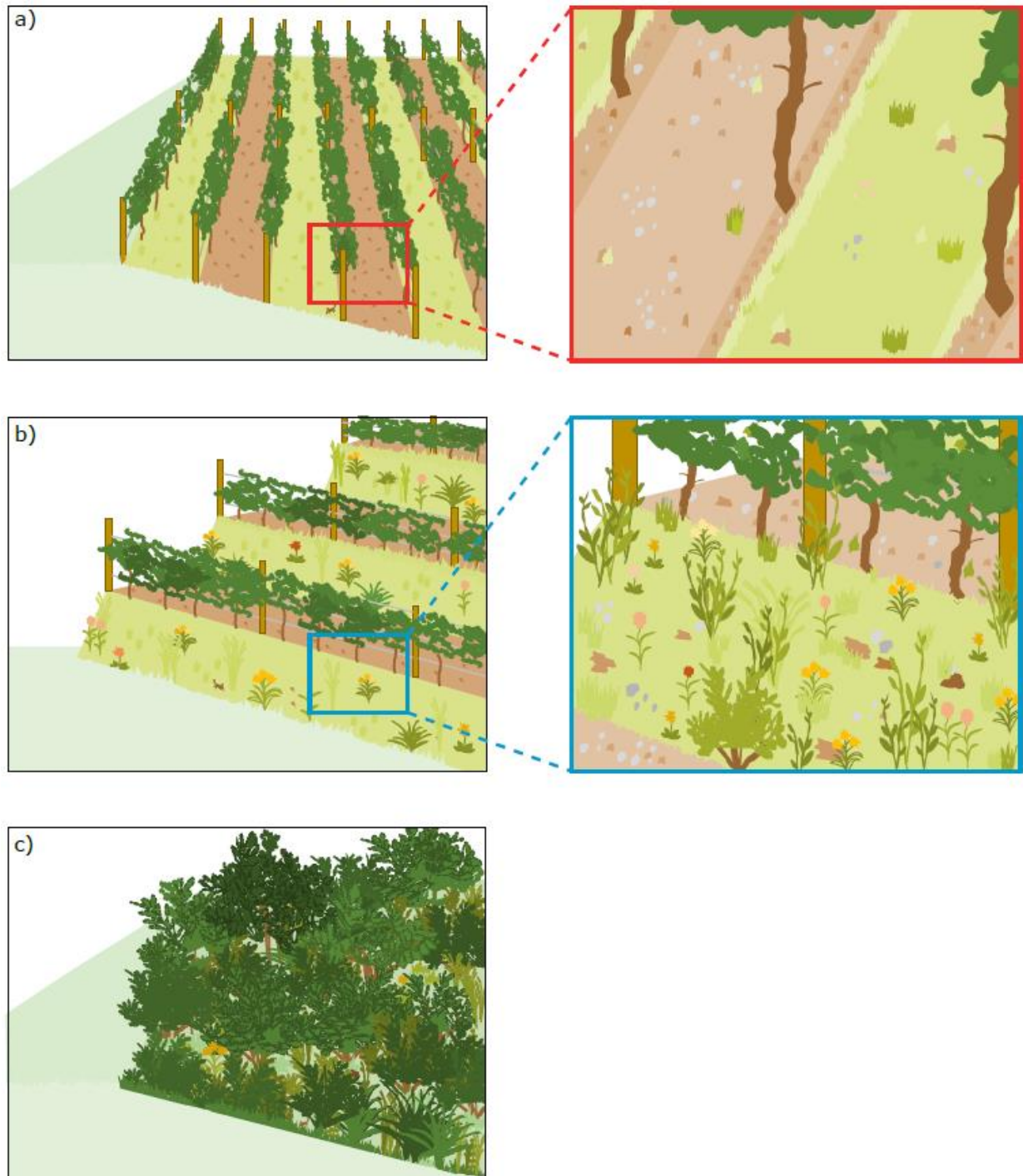


Figure 11: Three vineyard types were studied: a) vertically oriented vineyards that received alternating management with one inter-row being regularly tilled and the other one being permanently covered with vegetation, b) terraced vineyards with regularly tilled inter-rows and extensively managed vegetation on embankments, and c) vineyard fallows that were not managed and abandoned for at least 10 years.

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Vineyard types were arranged in triplets with each triplet including a vertically oriented vineyard, a terraced vineyard, and a vineyard fallow (Figure 11). We studied a total of 15 triplets (45 sites) belonging to 14 different winegrowers. Therefore, grape variety, age of the vines, and size of the vineyard area differed between sites. To ensure similar environmental conditions within triplets, sites were arranged close to each other. The inclination ranged from 17 ° to 42 °.

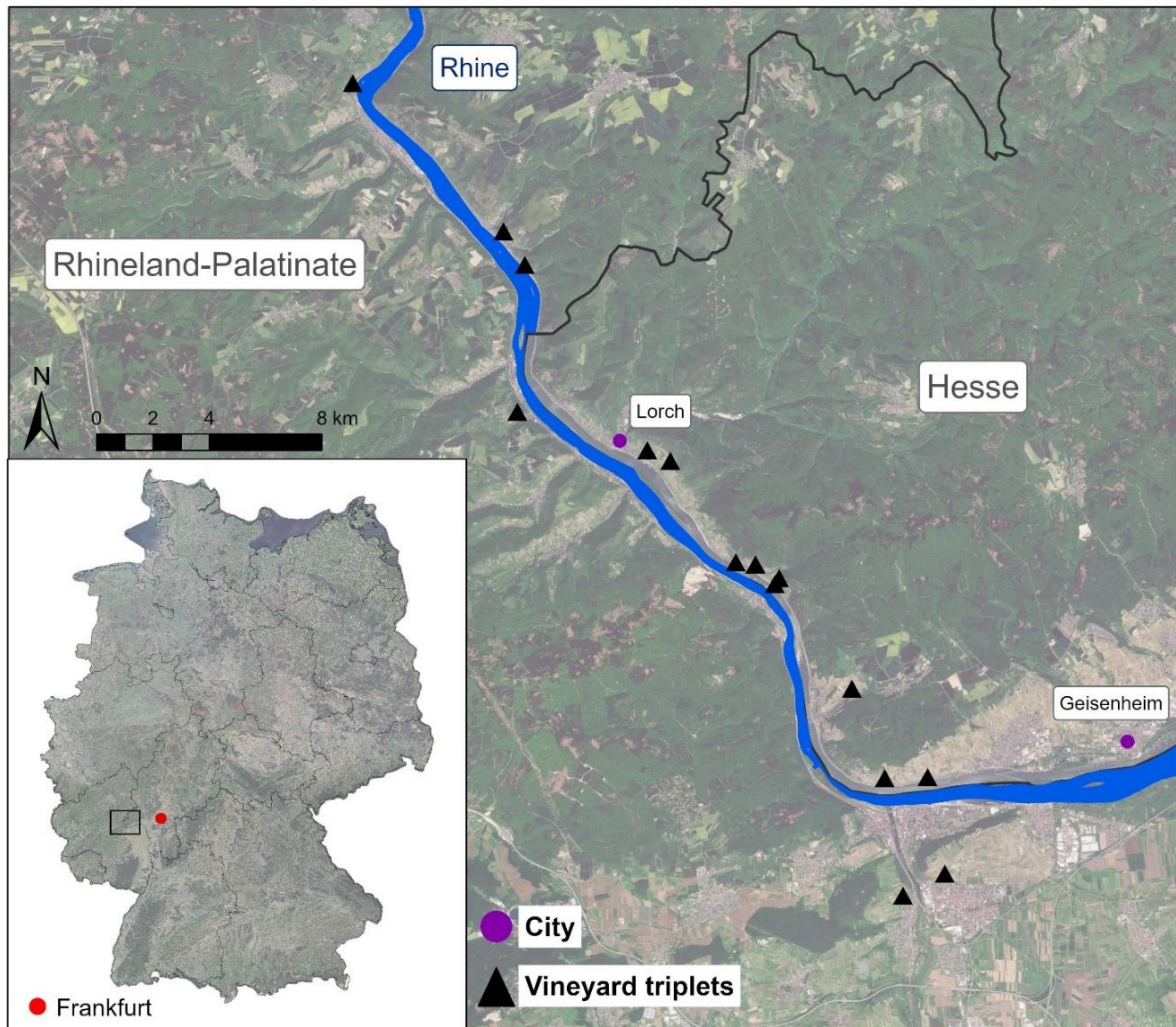


Figure 12: Location of study sites (15 vineyard triplets) in the Upper Middle Rhine Valley. © European Union, contains Copernicus Sentinel-2 data [2021], processed by the German Federal Agency for Cartography and Geodesy (BKG); GeoBasis-DE / BKG 2018.

4.3.2 Orthoptera sampling

Orthoptera sampling was carried out from late July to mid-August 2020 during sunny and warm weather conditions using suction sampling according to Mody et al. (2020). To vacuum a standardized area and to prevent Orthoptera from escaping before sampling, we used a biocenometer (an aluminium frame covered with fine mesh, 1 m × 1 m area, height 0.6 m).

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In managed vineyards (vertically oriented and terraced), we vacuumed a total area of 16 m² per site. To account for structural differences within vineyards we sampled vegetated and open inter-rows in vertically oriented vineyards and inter-rows and embankments in terraced vineyards (hereafter vineyard compartments) separately. For each of the two vineyard compartments per managed vineyard, we sampled 8 m². Sampling plots (1 m²) were spaced at a five-meter distance and split up into two neighbouring vineyard compartments of the same type in the centre of each site.

In addition, we also sampled the vine canopy at four randomly picked managed vineyard pairs by constantly vacuuming both sites of the canopy for one minute at two different positions each. Due to great structural differences in vineyard fallows (dense shrubby vegetation) compared to managed vineyards, Orthoptera sampling had to be conducted differently. For vineyard fallows, two sampling locations of about 2 m² were randomly selected in the centre and vacuumed for one minute each.

Orthoptera were directly determined after sampling using the determination keys of Fischer et al. (2020). Species that could not be determined in the field were anaesthetized with CO₂ and frozen until further processing (Fischer et al. 2020; Horstkotte et al. 1999). Juvenile Orthoptera that could not be reliably identified were excluded from the analysis.

4.3.3 Environmental variables and landscape analysis

In parallel with Orthoptera sampling, local vegetation parameters were recorded in two square rectangular plots of 1 × 1 m for every vineyard compartment and vineyard fallow. Within each plot, the percentage cover of bare ground, litter, vegetation, and shrubs was visually estimated. In this study, we defined litter as loose dead plant material that frequently occurred in high percentages due to dry and hot weather conditions and vegetation management (mulching). In addition, the average vegetation and shrub height was measured (two random measurements). For data analyses, mean values were calculated.

As landscape context might be a potential determinant of orthopterans (Marini et al. 2008), the cover of semi-natural habitats (mostly vineyard fallows in our study), forests and vineyards was quantified in a 150-m radius buffer around the study sites that included the slope range on which vines are cultivated, without including the Rhine. We additionally measured the distance from the centre position of each study site to the closest semi-natural habitat and forest. A more detailed description is given in Wersebeckmann et al. (2021).

4.3.4 Data analysis

For Orthoptera individuals, we calculated the density per m² for each vineyard type and vineyard compartment and assigned Orthoptera to sub-orders (Caelifera and Ensifera). To analyse differences

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between vineyard types for Orthoptera species richness, density, and local vegetation parameters, (generalized) linear mixed effect models (GLMM) were fitted with vineyard type and vineyard compartment as fixed effect and 'vineyard triplet' (factor with 15 levels) as a random effect to account for the nested design (function "glmmTMB", package glmmTMB; (Brooks et al. 2017)). Depending on the distribution of the response variable and residuals, models were fitted with Gaussian family, Poisson family for count data (species richness) or Negative binomial (over-dispersed count data) and Conway-Maxwell (under-dispersed count data) distribution. Post-hoc-tests (contrasts) were performed using the emmeans package (Lenth 2020). For vineyard compartments, analysis was done pairwise within the respective vineyard type (vertically oriented: vegetated vs. open interrow; terraced vineyard: inter-row vs. embankment). For use as a response variable, local vegetation parameters were log-transformed or square-root transformed to reduce skewness (Table 3, Table 4). To assess the effects of local vineyard and landscape factors on Orthoptera species richness and density, and on density of the two most abundant species within vineyard types and vineyard compartments, we built single GLMMs, due to multicollinearity among predictors, for each combination of the response variable and local and landscape parameters ($Y \sim \text{Intercept} + \text{predictor} + (1|\text{vineyard triplet})$).

To identify species associated with vineyard types and compartments, we performed an indicator species analysis using the IndVal procedure of Dufrêne and Legendre (1997). This analysis combines species abundance with its relative frequency of occurrence within the different vineyard types or compartments (function "multipatt", package indicpecies; (Cáceres and Legendre 2009)). P-values were obtained using a permutation test with 9999 permutations.

To unravel the influence of different vineyard types and compartments on Orthoptera assemblages, indirect ordination methods were applied using the vegan package (Oksanen et al. 2020). To start, we performed a Detrended Correspondence Analysis (DCA) and considered the length of gradient as a measure for the species turnover (Lepš and Šmilauer 2010). Since for vineyard types, the length of gradient was >3 (1st DCA axis: 3.38), the use of a linear-based ordination model was more appropriate and we performed a Principal Component Analysis (PCA) whereas for vineyard compartments a DCA (1st DCA axis: 4.02) was more suitable. Local vegetation and landscape parameters that were significantly related to the DCA and PCA axes ($p < 0.05$, based on a permutation test with 9999 permutations) were included post-hoc by projection. Before the analysis, all local vegetation and landscape variables were standardized to zero mean and unit variance (function "scale", package: vegan). The community data were $\log_{10}(x + 1)$ transformed to reduce the influence of dominant species. Additionally, species with less than two occurrences were excluded from the analysis, thus reducing the number of species from 15 to 7.

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All analyses were conducted in R version 3.6.3 (R Core Team 2020). Figures and maps were created with ggplot2 (Wickham 2016), cowplot (Wilke 2019), ArcGIS (ESRI 2019) and Inkscape version 1.2.1.

4.4 Results

In total, we sampled 254 Orthoptera individuals and 15 species (Table B. 1). Thereof, 7 species (174 individuals, 74.4 % of all ind.) belonged to Caelifera and 8 species (60 individuals, 25.6 % of all ind.) to the Ensifera suborder. *Chorthippus biguttulus* (Linnaeus, 1758) was the most abundant species (112 individuals, 44.0 % of all ind.), followed by *Oedipoda caerulescens* (Linnaeus, 1758) with 32 individuals (13.0 % of all ind.). Five species were only sampled once (*Chorthippus parallelus* (Zetterstedt, 1821), *Chorthippus dorsatus* (Zetterstedt, 1821), *Nemobius sylvestris* (Bosc, 1792), *Phaneroptera nana* (Fieber, 1853), *Pholidoptera griseoptera* (De Geer, 1773)). We collected three species of conservation concern, which are listed on the Red List of Orthoptera in Germany (Maas et al. 2011) (Table B. 1). In the vineyard canopy, we sampled only two species and three individuals (*L. punctatissima* (1), *O. pellucens* (2)) and therefore did not consider them for further analysis.

4.4.1 Local vegetation parameters

Local vegetation parameters did not differ significantly between managed vineyards (vertically oriented and terraced) but between managed vineyards and fallows (Table 3). Vegetation height and shrub cover were significantly higher, and bare ground and litter cover were significantly lower in fallows compared to managed vineyards. Vegetation cover was significantly higher in vertically oriented vineyards compared to fallows but did not differ from terraced vineyards (Table 3).

Table 3: Effects of vineyard type on local vegetation parameters (N = 15). Linear mixed effect models were used with vineyard triplet as a random factor. Different letters show significant differences between vineyard types ($p < 0.05$).

Variable	Managed vineyards		Abandoned vineyards
	Vertically oriented	Terrace	Fallow
Vegetation height ^{xx} [cm]	12.43 ^b ± 1.80	16.43 ^b ± 2.17	69.50 ^a ± 9.73
Bare ground cover [%]	36.87 ^a ± 5.45	39.98 ^a ± 4.71	11.83 ^b ± 2.33
Litter cover [%]	37.48 ^a ± 4.90	37.99 ^a ± 4.83	31.00 ^b ± 4.29
Vegetation cover ^{xx} [%]	22.80 ^a ± 4.05	16.03 ^{ab} ± 3.35	13.17 ^b ± 4.82
Shrub cover ^x [%]	2.80 ^b ± 1.09	6.00 ^b ± 2.13	44.00 ^a ± 6.49

^x Square-root transformed data were used for testing.

^{xx} Log-transformed data were used for testing.

Within managed vineyard types, local vegetation parameters differed significantly between compartments of the respective vineyard type (Table 4). In vertically oriented vineyards, bare ground cover was significantly higher in open inter-rows while vegetation height, litter, vegetation, and shrub cover were higher in vegetated inter-rows (Table 4). In terraced vineyards, vegetation height, litter, and shrub cover were significantly higher on embankments, while bare ground cover was significantly higher in inter-rows.

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Table 4: Effects of vineyard compartments on local vegetation parameters (N = 15). Comparisons were done pairwise within the respective vineyard type. Different letters show significant differences within the respective vineyard type ($p < 0.05$).

Variable	Vertically oriented		Terrace	
	Vegetated Inter-row	Open Inter-row	Embankment	Inter-Row
Vegetation height [cm]	15.37 ^a ± 2.92	9.50 ^b ± 1.13	23.87 ^a ± 3.82	8.98 ^b ± 2.09
Bare ground cover [%]	20.90 ^b ± 5.93	52.67 ^a ± 7.32	21.80 ^b ± 5.05	58.17 ^a ± 7.25
Litter cover [%]	46.50 ^a ± 6.4	28.13 ^b ± 6.07	50.33 ^a ± 6.56	25.65 ^b ± 5.49
Vegetation cover ^{xx} [%]	27.33 ^a ± 5.06	18.10 ^b ± 3.64	16.53 ± 4.75	15.52 ± 3.15
Shrub cover ^{xx} [%]	4.50 ^a ± 1.73	1.10 ^b ± 0.81	11.33 ^a ± 4.30	0.67 ^b ± 0.52

^{xx}Log transformed data were used for testing.

4.4.2 Orthoptera diversity in vineyard types

Orthoptera species richness differed significantly between vineyard types, with terraced vineyards having the highest and fallows having the lowest species richness (Figure 13 A). Vertically oriented vineyards had a significantly higher Orthoptera density than vineyard fallows with terraced vineyards in between (Figure 13 B). Caelifera species richness was significantly higher in managed vineyard types compared to vineyard fallows (Figure 13 C), while Caelifera density was significantly highest in vertically oriented vineyards and lowest in fallows (Figure 13 D). Ensifera species richness and density were highest in terraced vineyards compared to vertically oriented vineyards and fallows (Figure 13 E & F).

C. biguttulus dominated the community in vertically oriented vineyards and was the only indicator species assigned to this vineyard type (Table 5). For terraced vineyards, indicator species analysis revealed four species, three of which belong to the Ensifera-group (*P. albopunctata*, *P. falcata*, *O. pellucens*) and one belonging to the Caelifera-group (*O. caeruleus*) (Table 5). There were no species assigned to vineyard fallows.

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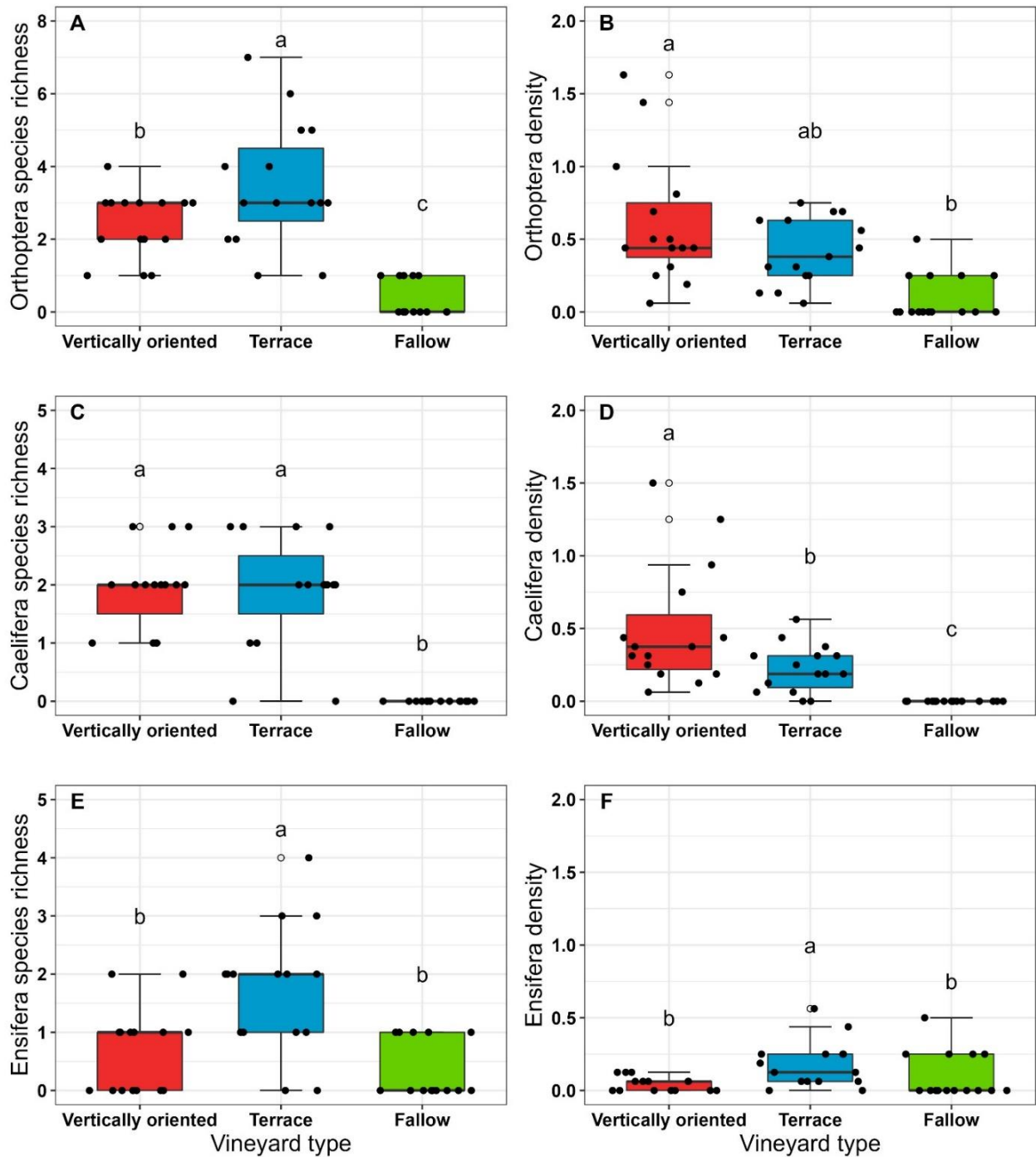


Figure 13: Differences in species richness of Orthoptera (A), Caelifera (C), Ensifera (E) and density of Orthoptera (B), Caelifera (D), and Ensifera (F) between vineyard types were analysed using (G)LMMs. Different letters indicate significant differences between vineyard types ($p < 0.05$).

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Table 5: Indicator Orthoptera species for the three vineyard types. Means and standard errors per vineyard type are displayed (N = 15). Species significantly associated with one vineyard type are printed in bold. Respective *p*-values are given (*p* < 0.05).

Species	Vertically oriented	Terrace	Fallow	<i>p</i>
<i>Platycleis albopunctata</i>	0.53 ± 0.17	1.00 ± 0.22	0.00 ± 0.00	0.0055
<i>Oecanthus pellucens</i>	0.13 ± 0.09	1.33 ± 0.53	0.20 ± 0.14	0.0056
<i>Oedipoda caerulescens</i>	0.93 ± 0.47	1.20 ± 0.44	0.00 ± 0.00	0.0451
<i>Phaneroptera falcata</i>	0.00 ± 0.00	0.33 ± 0.16	0.00 ± 0.00	0.0278
<i>Chorthippus biguttulus</i>	5.80 ± 1.63	1.67 ± 0.40	0.00 ± 0.00	0.0005

4.4.3. Orthoptera diversity in vineyard compartments

Within vertically oriented vineyards, neither species richness nor density was significantly different between vegetated and open inter-rows (Figure 14 A & B). For terraced vineyards, Orthoptera species richness was significantly higher on embankments compared to inter-rows, while Orthoptera density did not differ (Figure 14 A & B). There were no differences for Caelifera species richness and density between compartments (Figure 14 C & D), while for terraced vineyards Ensifera species richness and density were significantly higher on embankments compared to inter-rows (Figure 14 E & F). Indicator species analysis for compartments revealed two species associated with terrace embankments (Table 6).

Table 6: Indicator Orthoptera species for the four vineyard compartments. Means and standard errors per vineyard compartment are displayed (N = 15). Species significantly associated with one vineyard compartment are printed in bold (*p* < 0.05).

Species	Vertically oriented		Terrace		<i>p</i>
	Vegetated Inter-row	Open Inter-row	Embankment	Inter-Row	
<i>Platycleis albopunctata</i>	0.27 ± 0.15	0.27 ± 0.12	0.93 ± 0.23	0.07 ± 0.07	0.0023
<i>Oecanthus pellucens</i>	0.00 ± 0.00	0.07 ± 0.07	0.87 ± 0.35	0.40 ± 0.21	0.0103

4. Orthopteran diversity in steep slope vineyards: the role of vineyard type and vegetation management

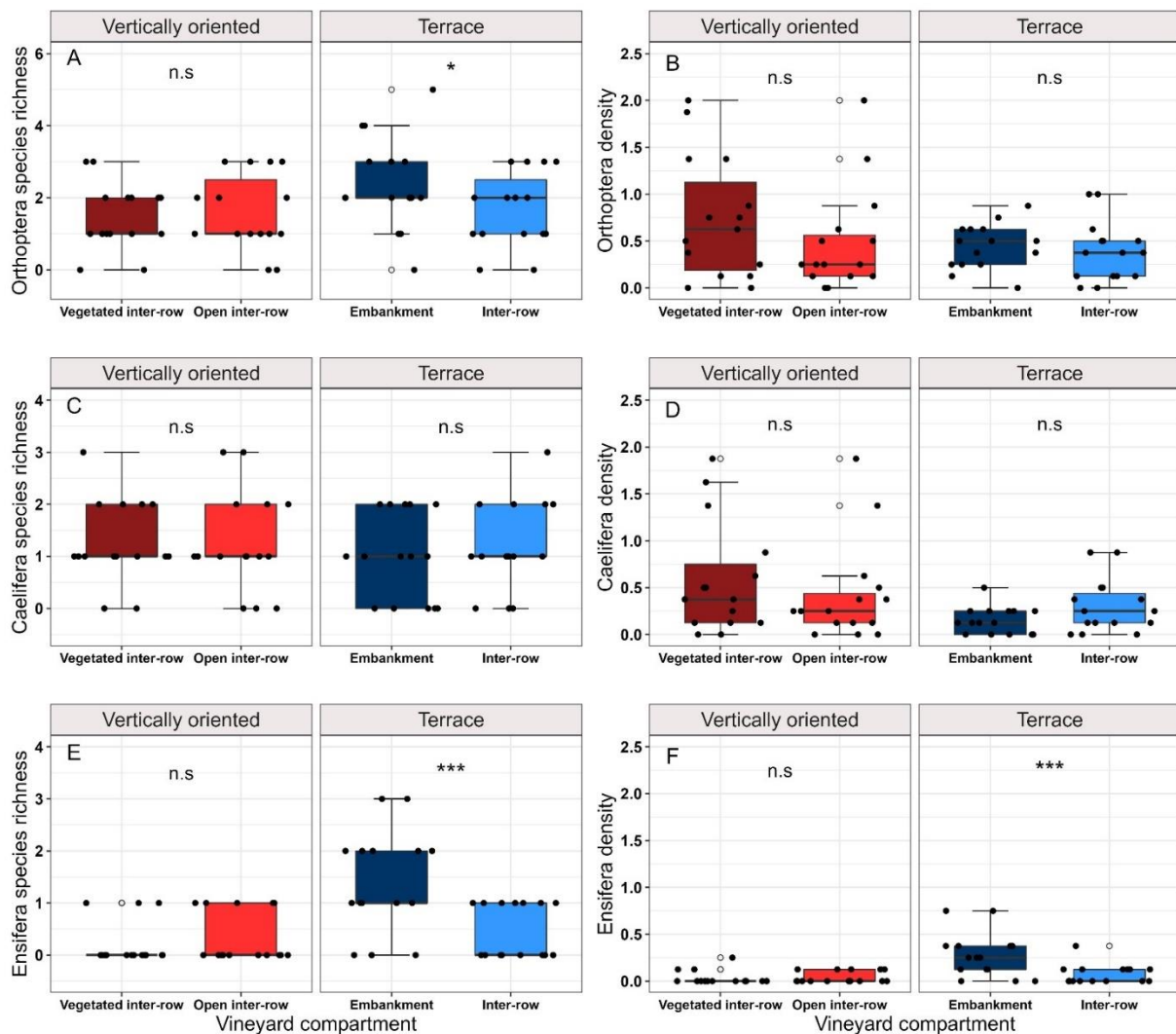


Figure 14: Boxplots show pairwise comparisons of Orthoptera species richness (A) and density (B), Caelifera species richness (C) and density (D), and Ensifera species richness (E) and density (F) between vineyard compartments of vertically oriented and terraced vineyards analysed using (G)LMMs. Asterisks indicate significance levels ($p < 0.05 = * < 0.001 = ***$). Nonsignificant p-values are indicated by n.s.

4.4.4. Effect of local and landscape parameters on Orthoptera

Local vegetation parameters significantly affected Orthoptera, Ensifera, and Caelifera species richness and density and density of the two most abundant species *C. biguttulus* and *O. caerulescens* in vineyard types and vineyard compartments (Table 7, Table B. 2, Table B. 3), whereas these effects were less pronounced for landscape parameters (Table 7, Table B. 2, Table B. 3). Among vineyard types, vegetation height and shrub cover negatively affected species richness of Orthoptera, Caelifera, and Ensifera and density of Orthoptera, Caelifera, and *C. biguttulus*, while bare ground cover positively affected Orthoptera and Caelifera species richness (Figure 15 B). Vegetation cover had a positive effect on Orthoptera, Caelifera, and *C. biguttulus* density. At the landscape scale, the proximity to semi-natural habitats (SNH) had a positive effect on Orthoptera and Ensifera species richness while Ensifera

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density was negatively affected by a cover of SNH but positively affected by vineyard cover in the surrounding landscape (Figure 15 A, Table 7, Table B. 2).

In vineyard compartments, vegetation height had a positive effect on Orthoptera and Ensifera species richness (Figure 15 C) and Ensifera density, while bare ground cover had a negative effect (Table B. 3). Ensifera and *C. biguttulus* density were positively affected by vegetation cover while *O. caerulescens* density was positively affected by bare ground cover (Figure 15 D). Litter cover positively affected Ensifera species richness but had negative effects on *O. caerulescens* density. At the landscape scale, SNH and forest cover positively and vineyard cover negatively affected Caelifera species richness while *O. caerulescens* was negatively affected by SNH cover in the surrounding landscape (Table B. 3).

Table 7: Effects of local vineyard and landscape parameters on Orthoptera species richness and density analyzed using vineyard types. The presented estimates and p-values are obtained from the single models $Y \sim \text{Intercept} + \text{Predictor}$ with 'vineyard triplet' as a random factor. R^2 marginal gives explained variation without and R^2 conditional with the random factor. Significant predictors ($p < 0.05$) are printed in bold; SNH: semi-natural habitat.

Dependent variable	Predictor	Estimate \pm SE	p-Value	R^2_{marg}	R^2_{cond}	AICc
Orthoptera species richness	SNH (%)	-0.04 \pm 0.12	0.7390	0.03	0.03	175.0
	Vineyard (%)	-0.01 \pm 0.13	0.9710	0.01	0.01	175.1
	Forest (%)	0.09 \pm 0.13	0.4620	0.02	0.02	174.6
	SNH distance (m)	0.25 \pm 0.09	0.0086	0.14	0.01	170.3
	Forest distance (m)	-0.15 \pm 0.12	0.1840	0.06	0.01	174.8
	Vegetation height (cm)	-0.85 \pm 0.23	0.0002	0.63	0.64	153.3
	Bare ground cover (%)	0.32 \pm 0.12	0.0081	0.18	0.18	168.2
	Vegetation cover (%)	0.21 \pm 0.12	0.0969	0.07	0.07	172.4
	Shrub cover (%)	-0.85 \pm 0.21	<0.0001	0.64	0.64	150.6
	Litter cover (%)	0.07 \pm 0.13	0.5820	0.01	0.01	174.8
Orthoptera density	SNH (%)	-0.01 \pm 0.05	0.7650	0.02	0.02	43.5
	Vineyard (%)	0.06 \pm 0.05	0.2910	0.03	0.03	42.5
	Forest (%)	-0.01 \pm 0.05	0.9150	0.01	0.01	43.6
	SNH distance (m)	0.08 \pm 0.05	0.1240	0.05	0.00	41.3
	Forest distance (m)	-0.02 \pm 0.05	0.6470	0.01	0.01	43.4
	Vegetation height (cm)	-0.18 \pm 0.05	0.0002	0.23	0.39	32.7
	Bare ground cover (%)	0.10 \pm 0.05	0.0585	0.08	0.12	40.2
	Vegetation cover (%)	0.12 \pm 0.05	0.0177	0.13	0.13	38.3
	Shrub cover (%)	-0.17 \pm 0.05	0.0004	0.21	0.31	33.2
	Litter cover (%)	-0.01 \pm 0.05	0.9560	0.01	0.01	43.3

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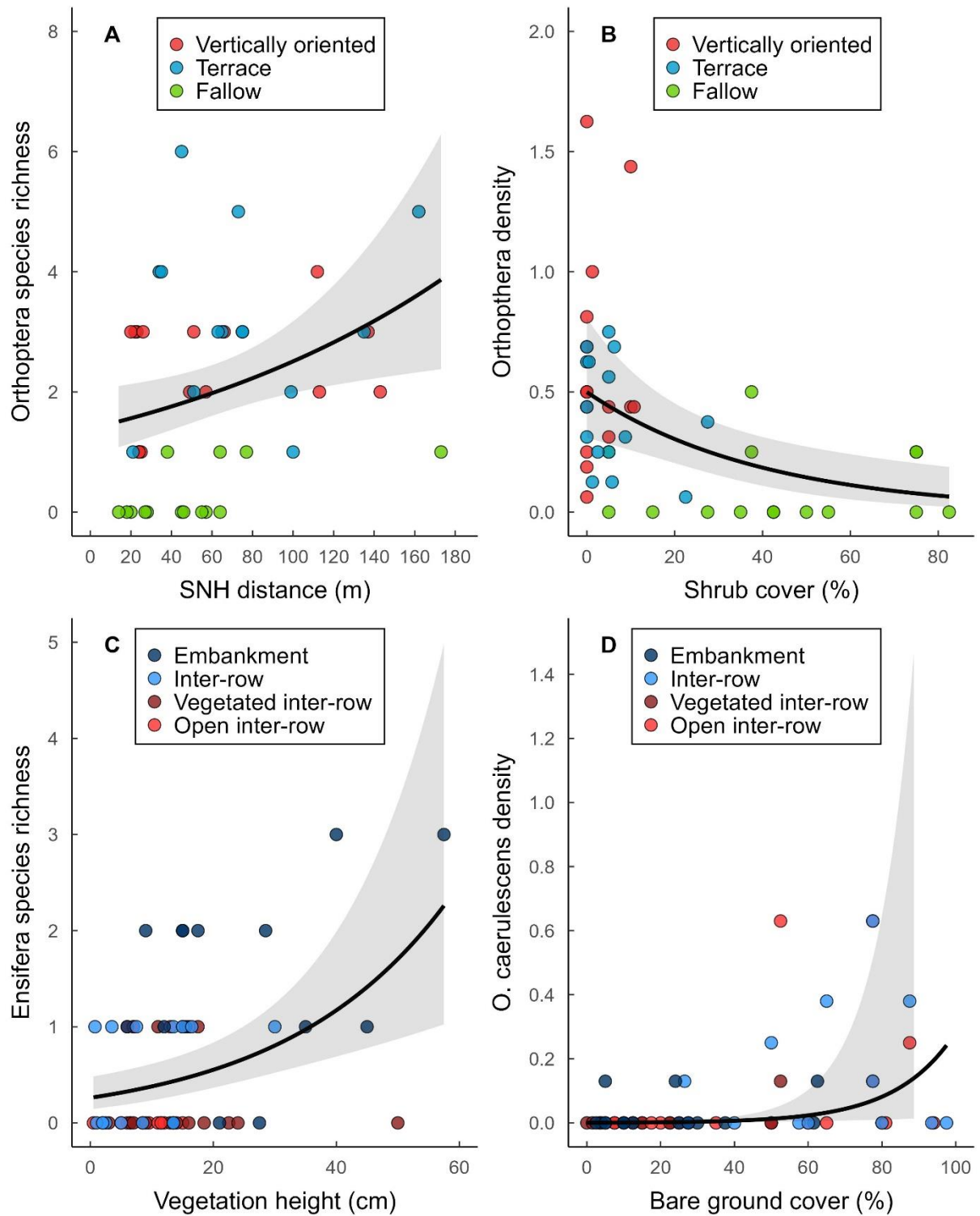


Figure 15: Relationship of Orthoptera species richness with SNH distance (A) and Orthoptera density with shrub cover (B) analysed using vineyard types, and Ensifera species richness with vegetation height (C) and *Oedipoda caerulescens* density with bare ground cover (D) analysed using vineyard compartments. Grey areas represent SE. See Table 7 (A and B) and Table B. 3 (C and D) for details.

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After excluding species with less than two occurrences from the analysis, only two fallow sites remained and revealed no differentiation of Orthoptera communities between vineyard types (Figure B. 1). In vineyard compartments, the first DCA-axis was mainly correlated with local environmental variables (Table B. 4). Inter-rows and open inter-rows were associated with higher bare ground cover and *O. caerulescens* whereas litter cover was more closely associated with embankments (Figure 16). Embankments, as well as the Ensifera species *O. pellucens*, *P. falcata*, and *P. albopunctata*, were positively correlated with the landscape variables distance to SNH and the percentage of surrounding vineyards on the second DCA-axis.

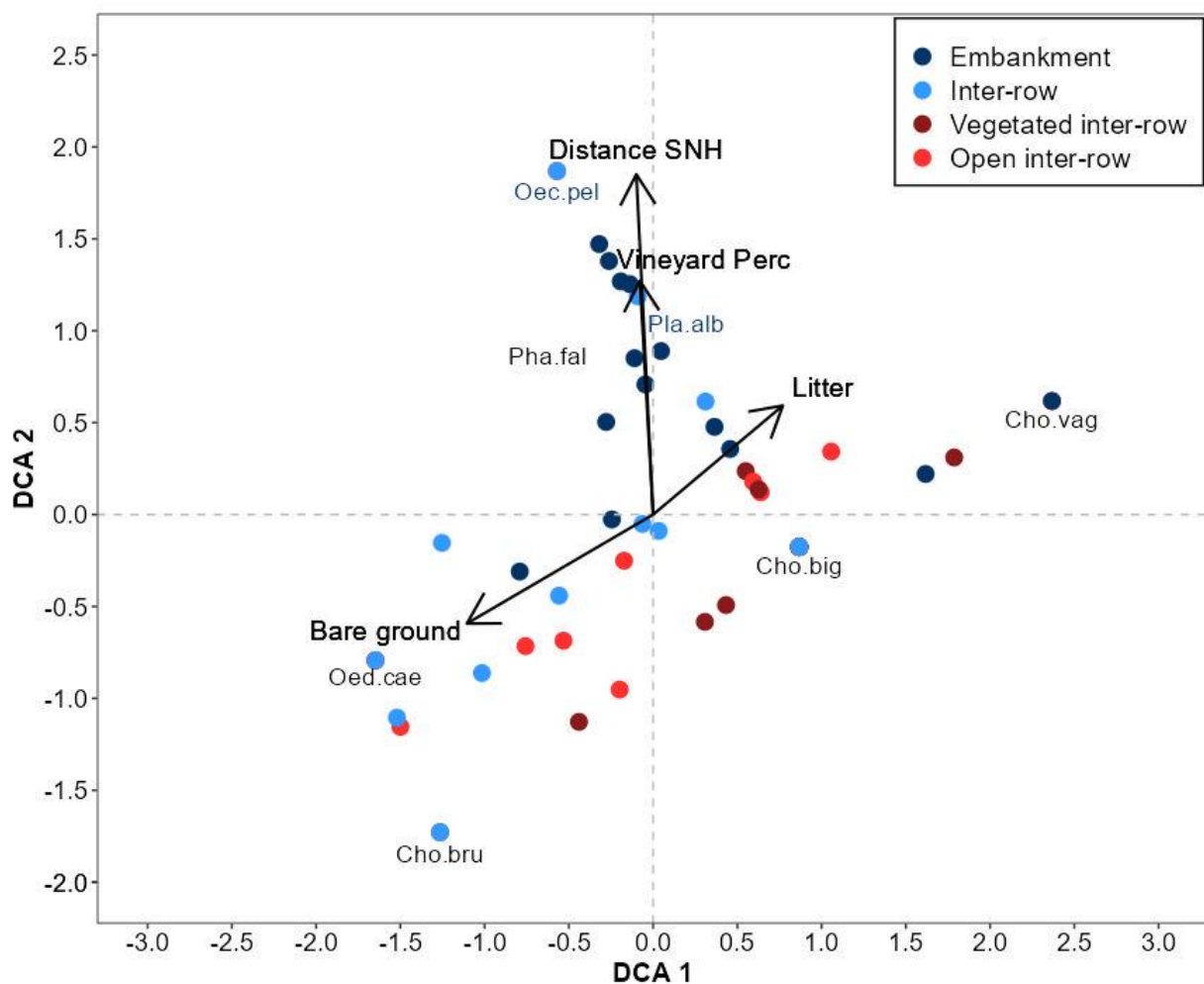


Figure 16: DCA results for Orthoptera species composition of vineyard compartments (length of gradient 1st DCA-axis: 4.02, 2nd DCA-axis: 3.6). Dots show scores for embankment (dark blue), inter-row (light blue), vegetated inter-row (dark red), and open inter-row (light red). Environmental and landscape variables that were significantly related to the DCA axes ($p < 0.05$, 9999 permutations) were included post-hoc by projection. Indicator species of terrace embankments are coloured in blue. For black-coloured species names, no assigned indicator values were available. Species abbreviations: Cho.big: *Chorthippus biguttulus*; Cho.bru: *Chorthippus brunneus*; Cho.vag: *Chorthippus vagans*; Oec.pel: *Oecanthus pellucens*; Oed.cae: *Oedipoda caerulescens*; Pha.alb: *Phaneroptera falcata*; Pla.alb: *Platycleis albopunctata*.

4.5. Discussion

The orthopteran species we recorded in our study represent approximately 20 % of the German Orthoptera fauna (Fischer et al. 2020). The species richness was similar to other studies investigating Orthoptera in temperate vineyards (10 species in Swiss vineyards, (Bruggisser et al. 2010)) while Orthoptera density in managed vineyards (density of $\bar{\varnothing}$ 0.47/m²) appeared to be lower than in other habitats such as grassland (3.5 to 7.4/m²)(Bundschuh et al. 2012; Branson 2011), field margin strips (0.9 to 3.3/m²)(Bundschuh et al. 2012), or urban roadside vegetation ($\bar{\varnothing}$ 1.5, max. 8 ind./m²)(Mody et al. 2020).

4.5.1. Effects of vineyard abandonment on Orthoptera diversity

In grasslands and heathlands, Orthoptera associated with open habitats areas negatively affected by older successional stages overgrown with woody vegetation resulting in lower species richness (Fartmann et al. 2012; Schirmel et al. 2011; Marini et al. 2009). In our study, we observed a similar pattern as all open-adapted Orthoptera species were missing in vineyard fallows and overall Orthoptera species richness and density were very low in comparison to actively managed vineyards. Orthoptera are cold-blooded organisms that require high ambient temperatures for optimal growth and reproduction (Willott and Hassall 1998), which is often interrelated with vegetation structure (Poniatowski and Fartmann 2008; Gardiner et al. 2002). In fallows, a high and dense shrub cover likely resulted in more shade and hence lower maximum temperatures near the ground. As pointed out by Bieringer and Zulka (2003), shading of the soil surface can be a serious threat for many thermophilous Caelifera species since they require sun-exposed bare ground and high ambient temperatures for completing their life cycles (Bieringer and Zulka 2003; van Wingerden 1991). In particular, for critically endangered *O. germanica* that colonizes hot and dry vegetation-free, and rocky habitats and is sensitive to denser vegetation, ongoing succession strongly reduces habitat quality (Fischer et al. 2020). On the contrary, Ensifera species were less affected by the presence of shrubs since they are less sensitive to cooler temperatures and denser vegetation structures for completing their life cycles (Bieringer and Zulka 2003) and are further known to better persist in transitional habitats with ongoing succession (Ortiz et al. 2021). However, the cover of SNHs (foremost vineyard fallows) in the surrounding landscape still negatively affected Ensifera density while Ensifera species number was positively correlated with an increased distance to SNH at the landscape scale, indicating that this group may be able to persist in these habitats but may still depend on grassy and herbaceous sites at the landscape scale (Steck et al. 2007). As forests are no typical habitat for most Orthopterans that are typically related to open grasslands, it is not surprising that we found no effects of forest cover in the surrounding landscape.

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Sampling Orthopterans in taller vegetation (>50 cm sward height) can be more problematic and the efficiency of sampling in fallows might be reduced by woody vegetation structures (Gardiner et al. 2005). However, we assume that unfavourable habitat conditions in fallows resulted in low species richness and densities rather than limited sampling efficiency. Accordingly, we assume that vineyard abandonment on steep slopes is a serious threat to Orthoptera diversity and in particular to the conservation of open-adapted and heat-loving Caelifera species. Nonetheless, fallows and woody elements in vineyards may have high conservation value for other groups such as cavity-nesting wild bees (Uzman et al. 2020) or birds (Pithon et al. 2016).

4.5.2. Effects of local vineyard management on Orthoptera diversity

Even though most Orthoptera species are polyphagous and do not depend on specific host plants for their survival, plant community composition is widely considered a determining factor for Orthoptera diversity (Bonari et al. 2017; Schaffers et al. 2008). A diverse plant community provides spatial and structural heterogeneity and hence various habitat niches but also distinct feeding opportunities and shelter against predators (Poniatowski et al. 2018; Badenhausser and Cordeau 2012; Gardiner et al. 2002). In our study, distinct vegetation structures were related to different management regimes within vertically oriented and terraced vineyards and determined Orthoptera community composition and contrasting responses of Caelifera and Ensifera species. Orthoptera communities of terrace embankments and vegetated inter-rows were mainly differentiated by distinct vegetation management. While embankment vegetation was mulched only once a year, and thus allowed for tall stands of grasses and herbs, the grass-dominated vegetation in vegetated inter-rows was kept short by regular mulching. The Orthoptera community on embankments mainly comprised Ensifera species that prefer a certain vegetation height and are further associated with the presence of shrubs such as *P. falcata*, but were still positively correlated with a greater distance to SNHs (foremost vineyard fallows) and cover of vineyards in the surrounding landscape since habitat conditions on vineyard fallows were less suitable (see 4.5.1). The high Orthoptera species richness on embankments was driven by a high Ensifera richness that was positively related to vegetation height. Taller vegetation on embankments is likely to increase shelter for large-bodied Ensifera species that are more prone to vertebrate predators than smaller Caelifera species (Batáry et al. 2007). Further, a mosaic of different microhabitats on embankments provided by bare ground patches in addition to taller vegetation met the needs of distinct life stages of Ensifera species such as *P. albopunctata*. This heat- and drought-loving species depends on bare ground patches for oviposition, sparsely vegetated habitats for their nymphs, and taller vegetation for adults (Ingrisch and Köhler 1998; Ingrisch 1978). In addition, thermophilic *O. pellucens* (Ensifera), typically found on south-exposed embankments and shrubby dry grasslands,

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likely profited from high insolation on embankments combined with tall vegetation and a small proportion of shrubs on embankments (Fischer et al. 2020).

The relatively high litter cover in our study was the result of withered vegetation due to heat and drought and residuals from mulching in vegetated inter-rows and embankments. Although litter is usually associated with unfavourable habitat conditions for Orthoptera, Gaigher and Samways (2010) found that a moderate litter cover created structural diversity in vineyards and supported different arthropod species. In addition, Bruggisser et al. (2010) suggested that mulching in vineyard inter-rows increased habitat heterogeneity and thus benefited Orthopteran diversity in Swiss vineyards.

The high density of Orthoptera and Caelifera in vertically oriented vineyards was driven by the dominance of *C. biguttulus*, a grass-feeding generalist that colonizes a broad range of habitats and seemed to be less sensitive to mulching management and short vegetation in vegetated inter-rows. These results coincide with findings from South African vineyards where Orthoptera diversity was low while Orthoptera density in inter-rows (comparable to vertically oriented vineyards) was high and mostly attributed to the dominance of one single species (Adu-Acheampong et al. 2016). Caelifera species richness was similar between terraced vineyards and vertically oriented vineyards, which can be related to the high availability of open and bare ground in both open inter-rows and inter-rows of terraces. For most thermophilic Caelifera species high temperatures and bare ground patches are essential for completing their life cycle (e.g. oviposition, embryonic development) (Uchida and Ushimaru 2014; Marini et al. 2009). Most of the individuals observed in open inter-rows belonged to *O. caerulescens*, which is known for its preference for sparsely vegetated, dry, and sun-exposed soils for basking (Ortis et al. 2021). Nevertheless, *O. caerulescens* depends on a certain amount of herbaceous vegetation for oviposition (Fischer et al. 2020) provided by embankments and vegetated inter-rows. Counterintuitively, when analysing vineyard compartments, Caelifera species richness showed a positive relationship with SNH and forest cover and a negative relationship with vineyard cover in the surrounding landscape. This effect might be explained by a more frequent occurrence of thermophilic *O. germanica* and *C. vargans* on sites with slate soils that heat up stronger but are even more affected by abandonment and subsequent natural forest recovery as wine growing at these sites is more effortful and less profitable.

To summarize, Orthoptera diversity in vineyards was supported by habitat heterogeneity created by alternating management within vineyards that provided different microhabitats at a site like bare ground, short and sparse, and taller vegetation and thus met the diverse requirements many Orthopterans have during different life stages (Bonari et al. 2017). Low-intensity management on embankments provided less disturbed vegetation structures and stands that were particularly

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beneficial for Ensifera diversity. Nevertheless, largescale mulching, even at low frequencies, causes high mortality rates in Orthopterans and other arthropods (Gaigher and Samways 2010; Ingrisch and Köhler 1998) and increases predation rates by vertebrates (Gardiner and Hassall 2009). These negative effects could be reduced by partial mulching that preserves temporarily uncut vegetation patches and hence provides refuge for orthopterans during and after the cuts (Ortis et al. 2021; Humbert et al. 2019). Maintaining and improving habitat quality for Orthopterans in vineyards is not only important for Orthoptera conservation but offers potential for natural pest control. Recently, in vineyards, omnivorous bush crickets (Tettigonidae) were observed to feed on pupae of the European grapevine moth *Lobesia botrana*, one of the major grapevine pests in Europe (Reich et al. 2021) and other species such as bush crickets (e.g. *Meconema meridionale*) are known to prey on pests such as leaf miners and chrysomelids (Grabenweger et al. 2005; Toepfer and Kuhlmann 2004).

4.6 Conclusion

Orthopteran diversity strongly decreased in vineyard fallows and all open-adapted species disappeared. Therefore, maintaining viticulture on steep slopes to preserve open structures is of great importance both on a local and landscape scale for the conservation of endangered orthopterans, but also for the conservation of habitats for other endangered species such as the Scarce swallowtail (*Iphiclides podalirius*). Faced with the challenges of cost disadvantages in steep slope viticulture, vineyard terracing provides a viable solution to maintaining wine growing economically sustainable and at the same time creating valuable habitats within the viticultural system. In particular, the extensive management and low degree of disturbance of the terrace embankments met the distinct habitat requirements that orthopterans have in different life stages by providing both open bare ground areas and vegetative cover.

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VW: Conceptualization, Data curation, Data analysis, Investigation, Methodology, Visualization, Writing - original draft, Writing - review & editing. **DW:** Species identification, writing—review and editing. **MHE:** Supervision, Writing - review & editing **IL:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing - review & editing.

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5.1 Abstract

1. Agricultural intensification and abandonment of traditional agricultural practices are main drivers of current insect declines. The resulting loss of feeding and nesting opportunities has led to a decrease in pollinator populations like wild bees. While the restoration of floral resources has been widely implemented in wild bee conservation, nesting resources, particularly for ground-nesting species, are barely considered.

2. We assessed wild bee diversity in a wine-growing area in Germany in 15 study sites along a soil gradient and evaluated whether wild bees were distinctly affected by different vineyard types (vertically oriented, terraced, abandoned), local conditions (e.g., shrub and flower cover), and landscape factors in response to divergent nesting needs (above-ground vs. ground-nesting).

3. We found that wild bees responded more strongly to the availability of nesting sites than to flower resources. While ground-nesting bees were determined by the suitability of soil aspects for nesting irrespective of vineyard management types, above ground-nesting bees profited from vineyard abandonment and shrub encroachment in vineyard fallows and were enhanced by the availability of seminatural habitats (SNH) in the surrounding landscape. In contrast, floral resource availability in managed vineyards had only marginal effects on above-ground-nesting bees.

4. *Synthesis and applications:* Life history traits like nesting strategies have long been neglected in wild bee conservation approaches, but proved to be highly relevant, especially for ground-nesting bees. For this, agri-environmental schemes can no longer solely focus on the restoration of floral resources, but should equally address nesting resources. Therefore, management efforts for enhancing wild bees in vineyard landscapes should aim at complementing nesting resources for ground-nesting bees (e.g., exposed bare ground patches) and above-ground-nesting bees (e.g. woody elements, hedges) in addition to floral resources. At the landscape level, conserving heterogeneous landscapes at a mixture of actively managed vineyards and semi-natural and woody elements is significant to maintain diverse bee communities.

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5.2 Introduction

Agricultural intensification associated with depletion and loss of semi-natural habitats and the use of agrochemicals are main drivers of a worldwide insect decline (Habel et al. 2019; Sánchez-Bayo and Wyckhuys 2019). In Europe, the shift of agricultural practices from traditional, low-input farming to intensive, large-scale productions in the second half of the twentieth century has especially threatened farmland species (Toivonen et al. 2016; Kleijn et al. 2009; Benton et al. 2002). However, when intensification is not profitable, e.g. in hilly and mountain areas, abandonment with subsequent forest encroachment degrades the ecological value for open-adapted species relying on extensive management (Sutcliffe et al. 2015; Marini et al. 2011).

In Germany, steep slope viticulture has shaped cultural landscapes of high aesthetic and conservation value such as the UNESCO world heritage site Upper Middle Rhine Valley (UMRV). However, over the last century, much of the traditional small-scale cultivation on dry-stone walls underwent a profound transformation. Due to land consolidation measures in the 1960s, vineyards were planted in a downhill direction on steep slopes to intensify productivity, increase mechanization, and the area under cultivation. Nevertheless, in recent decades these vineyards have increasingly been abandoned due to cost disadvantages in comparison to flat terrain sites (Strub and Loose 2021b). The progressive expansion of fallow land (up to 39 % in the Middle-Rhine Valley; 1987 – 2019)(Stoll and Schultz 2020) threatens the preservation of the cultural landscape as well as the flora and fauna adapted to viticultural cultivation and open landscapes.

To reduce further abandonment and keep management in steep slope viticulture sustainable, the reshaping of vertically oriented vineyards into modern vineyard terraces can be an economically viable approach (Strub and Loose 2021b). Here, vineyard rows run parallel to the hillside, thus reducing production costs by facilitating trafficability and manual production steps. Besides, a substantial area is composed of embankments that remain uncropped and are managed extensively and could therefore provide valuable habitats within the agricultural system (Wersebeckmann et al. 2021). In particular, when properly revegetated, species-rich embankment vegetation holds great potential to benefit flower-visiting insects by providing floral resources and nesting sites (Wersebeckmann et al. 2022).

Wild bees are entirely dependent on floral products for their food supply (Westrich 2019) and thus are important pollinators for agricultural crops (Garibaldi et al. 2013) and wild plants (Biesmeijer et al. 2006). The scarcity of floral resources in modern agricultural landscapes is, therefore, one of the predominant causes of declining wild bee populations (Sutter et al. 2017; Wood et al. 2017; Scheper et al. 2014). Thus, the implementation of flower plantings to enhance foraging resources has become a common method within agri-environmental schemes to promote wild bees. However, restored floral

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resources are only a partial substitute (Hevia et al. 2021) and their efficiency is much dependent on the landscape context and the proportion of semi-natural habitats (hereafter SNH) (Warzecha et al. 2021). Landscape elements like hedges (Garratt et al. 2017), fallows (Toivonen et al. 2016) or natural woodlands (Joshi et al. 2016) provide alternative habitats for foraging but also nesting and nest-building material (Westrich 2019) particularly for cavity-nesting bees (Bihaly et al. 2021; Uzman et al. 2020).

As central place foragers, wild bees depend on both floral resources and suitable nesting sites within species-specific flying distances as they need to return to their nests after foraging (Hofmann et al. 2020; Greenleaf et al. 2007). Accordingly, increasing floral resource availability alone does not concurrently translate into an increase in wild bee diversity (Harmon-Threatt 2020; Sardiñas et al. 2016). However, nesting resources have much less been considered as factors determining wild bee communities, persistence, and response to agricultural land use (Antoine and Forrest 2021; Ganser et al. 2021). Further, existing studies are mainly focused on cavity-nesting bees by the use of artificial trap nests (Leonard and Harmon-Threatt 2019; MacIvor 2017; MacIvor and Packer 2015) which only benefit a small proportion of common and widespread species (Drossart and Gérard 2020). In contrast, the majority of wild bees build nests below ground but yet studies are mainly based on observations of single species (Cane and Neff 2011). Hence, ecological and experimental studies on ground-nesting bees remain underrepresented (Orr et al. 2022). This might be due to the challenge to locate nests (Sardiñas and Kremen 2014) and the difficulty to apply passive collection measures for this group (Leonard and Harmon-Threatt 2019). Most recently, some studies have linked certain site characteristics such as exposed and sparsely vegetated soil as well as structurally open forms of agriculture (e.g. pasture, annual crops) with increases in ground-nesting bees (Brown et al. 2020; Carrié et al. 2018; Harrison et al. 2018). Until now, however, measures that target the provision of nesting resources, particularly for ground-nesting bees have been barely implemented in agricultural landscapes (but see Nichols et al. 2020; Williams et al. 2010). Our study contributes to filling this research gap and aims to include ecological trait information to help disentangle patterns of wild bee response to better guide conservation measures tailored to the demands of ground-nesting and above-ground nesting wild bees in agricultural landscapes.

5.3 Material and methods

5.3.1 Study sites

The study area is located in the wine-growing area of the Upper Middle Rhine Valley (UMRV) Germany, in Hesse (50.042342°N, 7.814533°E) and Rhineland-Palatinate (50.119139°N, 7.719275°E) (Figure 17). The climate is sub Atlantic with an annual mean temperature of 11.6 °C and total annual precipitation of 554 mm (Lorch, 2015–2019, weather station Hochschule Geisenheim).

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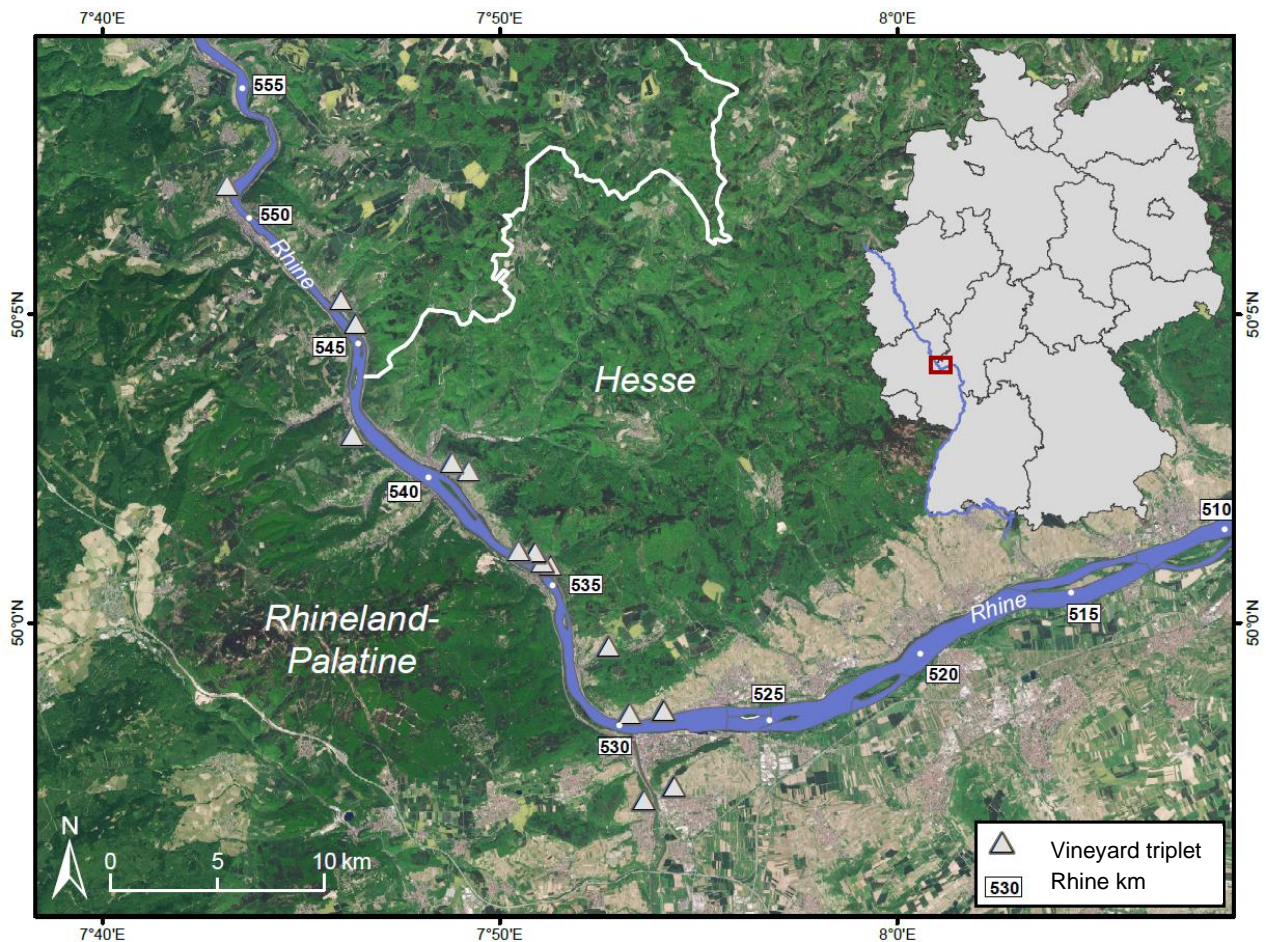


Figure 17: Location of study sites in the German wine-growing region of the Upper Middle Rhine Valley. Alongside the Rhine, 15 triplets of adjacent vertically oriented vineyards, terraced vineyards, and vineyard fallows were selected. © European Union, contains Copernicus Sentinel-2 data [2022], processed by the German Federal Agency for Cartography and Geodesy (BKG).

We selected 15 vineyard triplets, each including a terraced vineyard, a vertically oriented vineyard, and a vineyard fallow (hereafter summarized as vineyard types, see Figure C. 1 for details) for a total of 45 sampling plots. Within each triplet, plots were selected closely to each other to attain similar environmental conditions. The size of the vineyard, grape variety, and age of grapevines differed among sites. The vineyards were managed by 14 winegrowers under the standards of integrated pest management (EU Directive 2009/128/EC). For each vineyard, the total number of pesticide treatments (as the number of spraying events applying one or more substances) was measured based on the plant protection schemes for 2019. Pesticides encompassed fungicides and herbicides; insecticides were not applied. Terrace embankments were permanently covered with vegetation and usually mown once a year, while terrace inter-rows were regularly tilled. Inter-rows of vertically oriented vineyards received an alternating tillage treatment, i.e., every second inter-row was tilled at least once a year while the other inter-row was not tilled, but permanently covered with vegetation. Vineyard fallows were predominantly overgrown with shrubby vegetation such as blackberry (*Rubus fruticosus* agg.), dog rose

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(*Rosa canina* agg.), wild cherry (*Prunus avium* (L.) L.), or midland hawthorn (*Crataegus laevigata* (Poir.) DC., s. l.) and were at least abandoned for 10 years.

An official permission for sampling bees was given by the Regional Administrative Council in charge (Struktur- und Genehmigungsdirektion Süd and Nord, Rheingau-Taunus Kreis). An ethical approval was not required.

5.3.2 Wild bee sampling

Wild bee sampling was carried out from April to August 2019 in a total of three sampling rounds. At each sampling round, traps were exposed for three consecutive days per plot (18th – 20th April, 28th – 30th June, 23rd – 26th August) under dry and warm weather conditions (>15 °C) with low wind speeds. For each plot and sampling round, we used a set of three differently coloured pan traps with a diameter of 15.6 cm with 500 ml; the inside was painted with blue, white, and yellow UV-reflecting paints (Sparvar Leuchtfarbe, Spray-Color GmbH, Merzenich) and filled with water with a small drop of odourless detergent. Traps were placed in the vineyard centre at a distance of 3 m from each other and adjusted at the level of the surrounding vegetation since bees seem to collect floral resources within horizontal strata (Waddington 1979). To reduce the prominent contrast of pan traps on bare ground in inter-rows of vertically oriented vineyards, traps were placed in the inter-row with the higher vegetation and flower cover. In terraced vineyards, traps were placed on embankments, and in fallows, traps were placed in the centre at shrub height.

Wild bees were identified to species level except for those of the species complexes of *Bombus terrestris* agg. (*Bombus lucorum* and *B. terrestris*), *B. hortorum* agg. (*B. hortorum* and *B. ruderatus*) and *Halictus simplex* agg. (*Halictus langobardicus* and *H. simplex*) (Table C. 1) or excluded from species-level analysis (3 individuals). Honey bees (*Apis mellifera*) were excluded from the analysis as their abundance greatly depends on nearby beekeeping. All samples per site were pooled over the three sampling rounds. We assigned species to be ground-nesting or above-ground-nesting following Westrich (2019). Parasitic species, do not build their nests but rather depend on their hosts and were therefore not considered as having nesting preferences (Antoine and Forrest 2021).

5.3.3 Environmental variables

Environmental parameters were assessed for each sampling round in parallel with wild bee sampling (April, June, and August 2019). We recorded local vegetation parameters for each plot in two randomly chosen rectangles of 0.5 × 2 m for managed vineyards and two rectangles of 1 × 1 m for fallows around the traps (two samplings per plot and sampling round). Within each rectangle, we visually estimated the percentage cover of bare ground, herbaceous vegetation, shrubs, and the cover of all blooming-coloured plants. We determined all flowering plants to species level and summarized them as the total

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number of flowering plant species in each rectangle. In addition, we measured the height of vegetation and shrubs (five random measurements) within each rectangle. Mean values were calculated and averaged over the three sampling rounds.

To account for differences in the soil composition we defined five categories (hereafter referred to as soil 1 - 5) along a gradient from fine soil to coarse gravel particles. We visually estimated the proportion and size of fine (< 2 mm) and coarse soil particles in a rectangle of 0.4 × 0.4 m. Soil 1 and 2 predominantly had fine particles and less than 40 % gravel, while soil 3 – 5 had a minimum of 40 % gravel that increased in size from soil 3 (max. size of 1 cm), soil 4 (1–4 cm) to soil 5 (min. size of 5 cm) (Figure C. 2).

5.3.4 Landscape analysis

To analyse the landscape structure we chose a 150 m radius around each study site, as female bees forage mostly within 125 to 150 meters from the nest when they are not forced to fly further (Hofmann et al. 2020). Within each radius, we calculated the area of semi-natural habitats, forests, and vineyards. SNH elements encompassed woody habitats such as vineyard fallows (predominantly) and hedges and herbaceous habitats (meadows or field margins with extensive vegetation). As a reference, we used the digital landscape model for Germany from 2009 (DLM-DE 2009), which we matched and updated with orthophotos (resolution of 40 ×40 cm) provided by the Hessian State Office of Land Management and the Surveying and Geographic Information Office Rhineland-Palatinate. The analysis was carried out using ArcGIS 10.7.1. Additionally, we measured the distance from the vineyard centre to the closest SNH and forest using Google Earth Pro.

5.3.5 Data analysis

All statistical analyses were computed in R 3.6.3 (R Core Team 2020). Since landscape factors and soil composition altered alongside the river current, we used Rhine kilometres (a measure of overall river channel length) as a proxy to display altering soil and environmental conditions (Figure C. 3). We used Pearson correlation coefficients (function: `cor.test`) to describe the alteration of landscape parameters, soil aspect, bee species richness, bee abundance, and nesting traits with the river current (Rhine km).

We choose (generalized) linear mixed effect models (GLMMs) for analysis. Data exploration was conducted according to Zuur et al. (2010). In the first step, to characterise differences between vineyard types GLMMs were fitted with vineyard type as fixed and vineyard triplet (factor with 15 levels) as random effect (package: `glmmTMB`; (Brooks et al. 2017)). For the model containing spraying events as a response variable, “winegrower” (factor with 14 levels) was used as a random factor. Depending on the distribution of the response variable and residuals, models were fitted with Gaussian family, Poisson family for count data or Negative binomial (over-dispersed count data) and Conway-Maxwell

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(under-dispersed count data) distribution, see Table C. 2 and Table C. 3 for details. Post-hoc-pairwise comparisons (Tukey method) were performed using the emmeans package (Lenth 2020).

In the second step, to identify drivers of bee species richness, bee abundance, threatened bees, and nesting traits, we choose manual stepwise model selection of appropriate GLMMs via the AICc-criterion. Before model building, the explanatory variable set (all local and landscape factors) was reduced using a PCA. As loadings of individual variables showed that landscape factors were correlated with the first and local factors were correlated with the second PCA-axis, we decided to set up two different models, one for local and one for landscape factors. For the model on local factors, the final variable set was reduced to shrub cover, number of flowering species, bare ground cover, and flower cover while the landscape model was reduced to vineyard cover, soil, SNH cover, and SNH distance after excluding variables with a variance inflation factor (VIF) > 3. Numerical explanatory variables were scaled and centred before testing. Model selections were done manually via the Akaike information criterion for small sample sizes (AICc) using the drop1-function (package: MuMIn; Barton, 2020). Conditional and marginal R^2 s were calculated (package: sjstats; Lüdecke, 2020). To analyse the effects of soil on ground-nesting bees separately we performed GLMs for comparison and summarised bee species richness and abundance per triplet, as soil compositions were similar within triplets.

We performed a redundancy analysis (RDA) as a direct ordination method to explore patterns in bee community composition in relation to local and landscape factors using the vegan package (Oksanen et al. 2020). To reduce the influence of dominant species, species with less than three occurrences were excluded from the analysis, thus reducing the number of species from 115 to 61 in total. The model included $\log_{10}(x + 1)$ transformed bee community data as species matrix and local and landscape factors as explanatory variables. All environmental and landscape variables were standardized to zero mean and unit variance before the analysis (function “scale”, package: vegan).

5.4 Results

Overall, we sampled 3385 wild bees belonging to 115 species; 29 species of conservation concern. Of all species, 61 species and 2870 individuals (85 % of all individuals) were ground-nesting, 39 species and 456 individuals (13.5% of all ind.) were above ground-nesting, and 14 species and 49 individuals (1.5% of all ind.) lived parasitically. The three most abundant species were all ground-nesting: *Lasioglossum morio* (12.4%), *L. laticeps* (12.2%), and *L. malachurum* (12.1%) (Table C. 1).

5.4.1 Differences between vineyard types

Local vegetation parameters differed significantly between vineyard types (Table C. 2). Terraced vineyards had the highest vegetation and flower cover and flower species richness compared to vertically oriented vineyards and vineyard fallows. Vertically oriented vineyards had no shrub cover and

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a higher bare ground cover than terraced vineyards and fallows. On average, vineyard fallows had a higher shrub cover and shrub height than the two managed vineyards. Vegetation was higher in terraced vineyards and vineyard fallows compared to vertically oriented vineyards. The number of spraying events did not differ between vertically oriented and terraced vineyards.

Species richness of wild bees was significantly higher in vineyard fallows compared to vertically oriented vineyards (Figure C. 4 A, Table C. 3) while there was no difference in wild bee abundance between vineyard types (Figure C. 4 B). Above-ground nesting species richness and abundance were significantly higher in vineyard fallows than in both managed vineyard types (Figure 18, Table C. 3). There was no difference between vineyard types for species richness and abundance of ground-nesting (Figure 18 B, D) and threatened bees (Figure C. 4 C, D).

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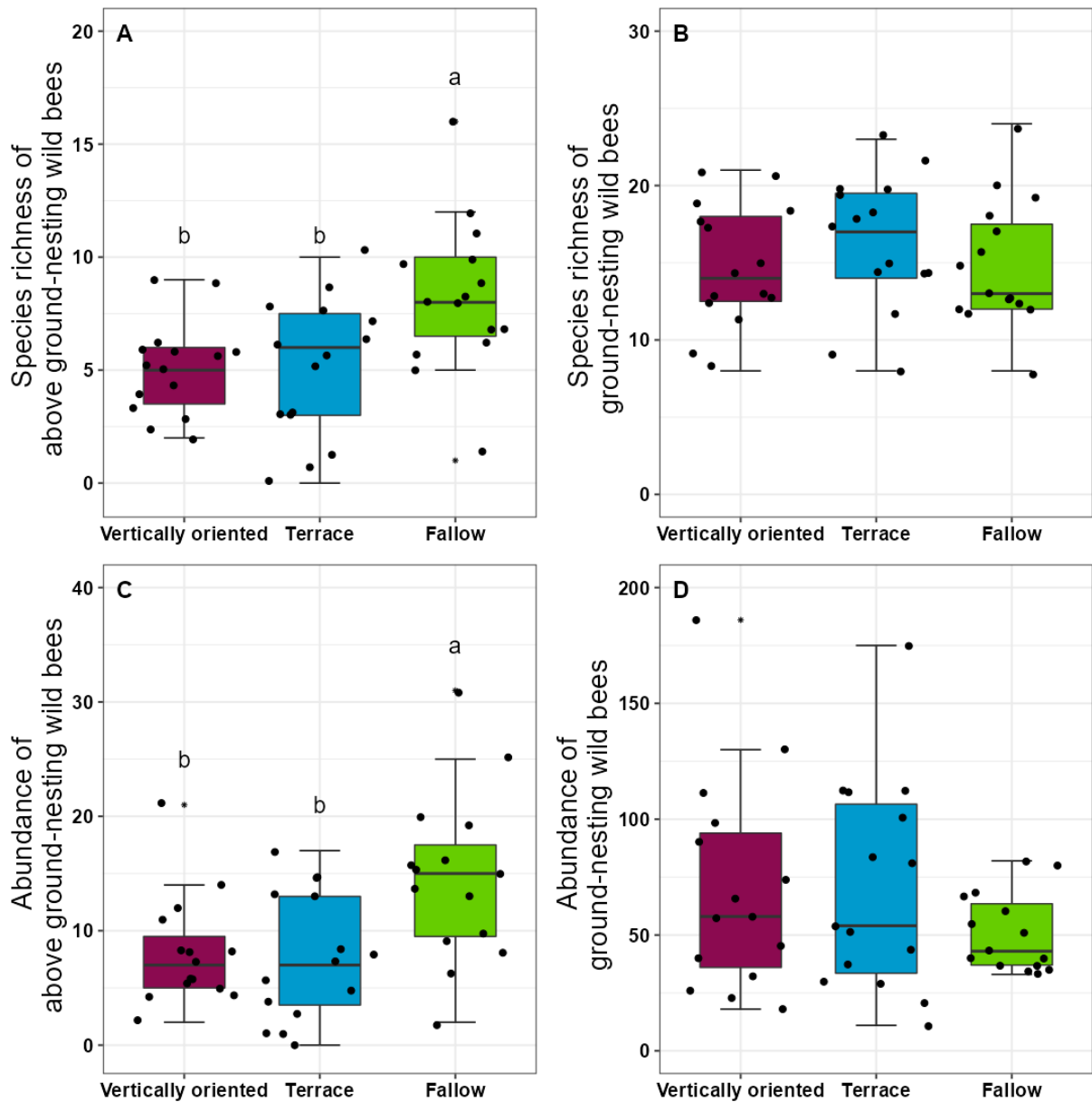


Figure 18: Differences between vineyard types for species richness of above ground-nesting (A), ground-nesting wild bees (B), and abundances of above ground-nesting bees (C) and ground-nesting bees (D) analysed using GLMMs. Each data point represents the number of species or individuals for the respective vineyard type (N = 15). Different letters indicate significant differences between vineyard types ($p < 0.05$). Respective p-values are given in Table C. 3.

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5.4.2 Influence of landscape and local parameters

Species richness of above-ground nesting bees (Figure C. 6 A) was positively correlated with proximity and increasing cover of woody structures (SNH and forest) alongside Rhine kilometres (Figure C. 3 B-E). In contrast, overall bee species richness (Figure C. 5 A), bee abundance (Figure C. 5 B), ground-nesting species richness (Figure C. 6 C), and ground-nesting abundance (Figure C. 6 D) were negatively correlated with woody structures and coarser soil particles (Figure C. 3). Above-ground nesting bee abundance showed no correlation with Rhine kilometres (Figure C. 6 B).

We found contrasting effects of local and landscape parameters on bee species richness, abundance, nesting traits, and threatened bees (Table 8). On the local scale, we found positive trends of shrub cover on bee species richness ($E = 0.07 \pm 0.03$, $p = 0.0347$) and above-ground-nesting species richness ($E = 0.20 \pm 0.06$, $p = 0.0007$) and abundance ($E = 0.29 \pm 0.08$, $p = 0.0007$), while for ground-nesting bee abundance flower cover had a positive effect ($E = 0.17 \pm 0.07$, $p = 0.0115$). No significant effects of local factors were detected for ground-nesting species richness and threatened bees. On the landscape scale vineyard cover positively affected bee species richness ($E = 0.19 \pm 0.05$, $p = 0.0003$), bee abundance ($E = 0.31 \pm 0.07$, $p = 0.0002$), ground-nesting species richness ($E = 0.22 \pm 0.03$, $p < 0.0001$) and abundance ($E = 0.40 \pm 0.08$, $p < 0.0001$, Figure 19 B) as well as threatened species richness ($E = 0.25 \pm 0.05$, $p < 0.0001$) and abundance ($E = 0.67 \pm 0.18$, $p = 0.0002$). SNH cover in the surrounding landscape had a positive effect on bee species richness ($E = 0.10 \pm 0.03$, $p = 0.0013$), above-ground-nesting species richness ($E = 0.39 \pm 0.10$, $p < 0.0001$), and abundance ($E = 0.44 \pm 0.14$, $p = 0.0019$, Figure 19 A) while the distance to SNH had a negative effect on above-ground-nesting abundance ($E = -0.27 \pm 0.11$, $p = 0.0491$). Analysis of ground-nesting bees and soil composition showed that the species richness of ground-nesting bees differed significantly between soil 1 (fine soil particles) and soil 5 (coarse gravel) (Figure 19 C). Ground-nesting wild bees were significantly more abundant in soil 1 (Figure 19 D).

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Table 8: Effects of local vineyard (local model) and landscape factors (landscape model) on bee species richness, bee abundance, nesting traits, and threatened bees. The presented estimates and p-values are obtained from the most parsimonious model after stepwise model selection. Marginal R^2 gives explained variation without -, conditional R^2 with random factor. Significant predictors ($p < 0.05$) are printed in bold.

Dependent variable	Predictor	Estimate \pm SE	p-Value	R^2_{marg}	R^2_{cond}	AICc
Local model: $Y \sim \text{Intercept} + \text{shrub cover} + \text{Nr. of flowering species} + \text{bare ground cover} + \text{flower cover} + (1 \text{triplet})$						
Wild bee species richness	Shrub cover (%)	0.07 \pm 0.03	0.0347	0.08	0.23	272.5
Wild bee abundance	Flower cover (%)	0.12 \pm 0.06	0.05361	0.06	0.52	441.5
Above-ground-nesting species richness	Shrub cover (%)	0.20 \pm 0.06	0.0007	0.15	0.42	228.9
Above-ground-nesting abundance	Shrub cover (%)	0.29 \pm 0.08	0.0007	0.19	0.40	287.7
Ground-nesting abundance	Flower cover (%)	0.17 \pm 0.07	0.0115	0.08	0.63	430.5
Landscape model: $Y \sim \text{Intercept} + \text{vineyard cover} + \text{soil} + \text{SNH cover} + \text{SNH distance} + (1 \text{triplet})$						
Wild bee species richness	Vineyard (%) SNH (%)	0.19 \pm 0.05 0.10 \pm 0.03	0.0003 0.0013	0.27	0.29	268.8
Wild bee abundance	Vineyard (%)	0.31 \pm 0.07	0.0002	0.39	0.51	431.8
Above-ground-nesting species richness	Soil SNH (%)	-0.15 \pm 0.10 0.39 \pm 0.10	0.1352 <0.0001	0.34	0.41	224.7
Above-ground-nesting abundance	Vineyard (%) SNH (%) SNH distance (m)	0.26 \pm 0.14 0.44 \pm 0.14 -0.27 \pm 0.11	0.0652 0.0019 0.0491	0.39	0.42	284.4
Ground-nesting species richness	Vineyard (%)	0.22 \pm 0.03	<0.0001	0.10	0.10	219.8
Ground-nesting abundance	Vineyard (%)	0.40 \pm 0.08	<0.0001	0.46	0.60	421.1
Threatened bee species richness	Vineyard (%)	0.25 \pm 0.05	<0.0001	0.16	0.00	143.0
Threatened bee abundance	Vineyard (%) SNH distance (m)	0.67 \pm 0.18 -0.19 \pm 0.13	0.0002 0.1292	0.39	0.69	296.3

5. Contrasting effects of vineyard type, soil and landscape factors on ground- versus above-ground nesting bees

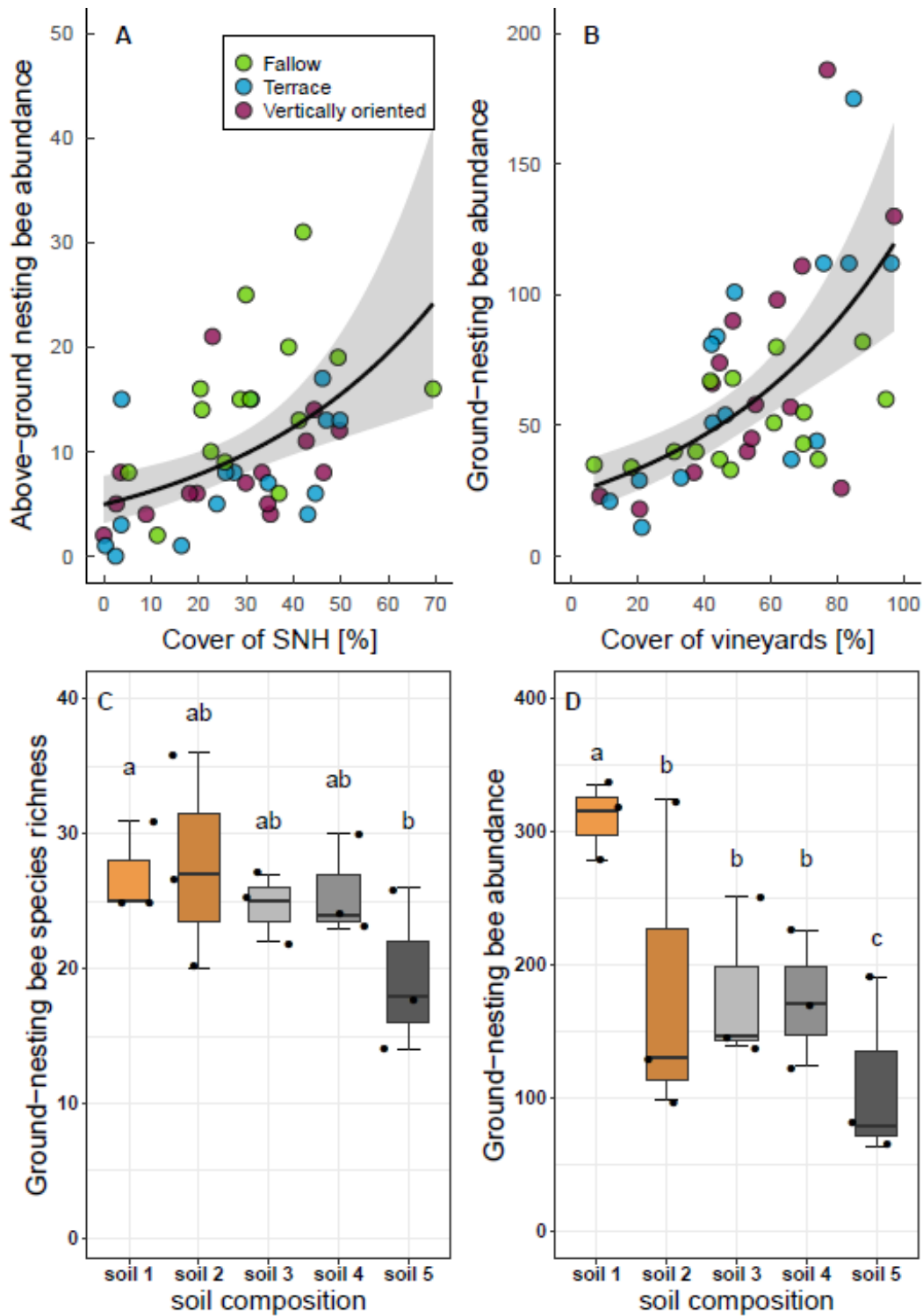


Figure 19: Relationship of above-ground-nesting bee abundance (A) with SNH cover and ground-nesting bee abundance (B) with vineyard cover within a radius of 150m. Grey areas represent SE. Green dots represent vineyard fallows, blue dots represent terraced vineyards and pink dots represent vertically oriented vineyards respectively. See Table C. 3 for details. Boxplots show differences in ground-nesting species richness (C), and individuals (D) between soil composition analysed using GLMs. Each data point represents the number of species (C) and individuals (D) for one vineyard triplet (N = 15). Different letters indicate significant differences between soils ($p < 0.05$).

5. Contrasting effects of vineyard type, soil and landscape factors on ground- versus above-ground nesting bees

RDA on bee species composition in relation to local and landscape factors revealed a strong correlation of landscape factors that changed alongside the Rhine with the first RDA-Axis and clustering of Rhine kilometres, and soil composition respectively (Figure 20, Table C. 4). The second axis mainly correlated with local factors and revealed differentiation between vineyard fallows and managed vineyards (vertically oriented, terraced), while local factors related to vineyard types mainly correlated with the second RDA-axis. We coloured species names in Figure 20 C according to their nesting traits and by comparing Figure 20 A, C, and B, ground-nesting species are related to the first axis and landscape factors such as vineyard cover, while above-ground-nesting species are more closely related to the second axis and variables related to vineyard fallows such as shrub cover.

5. Contrasting effects of vineyard type, soil and landscape factors on ground- versus above-ground nesting bees

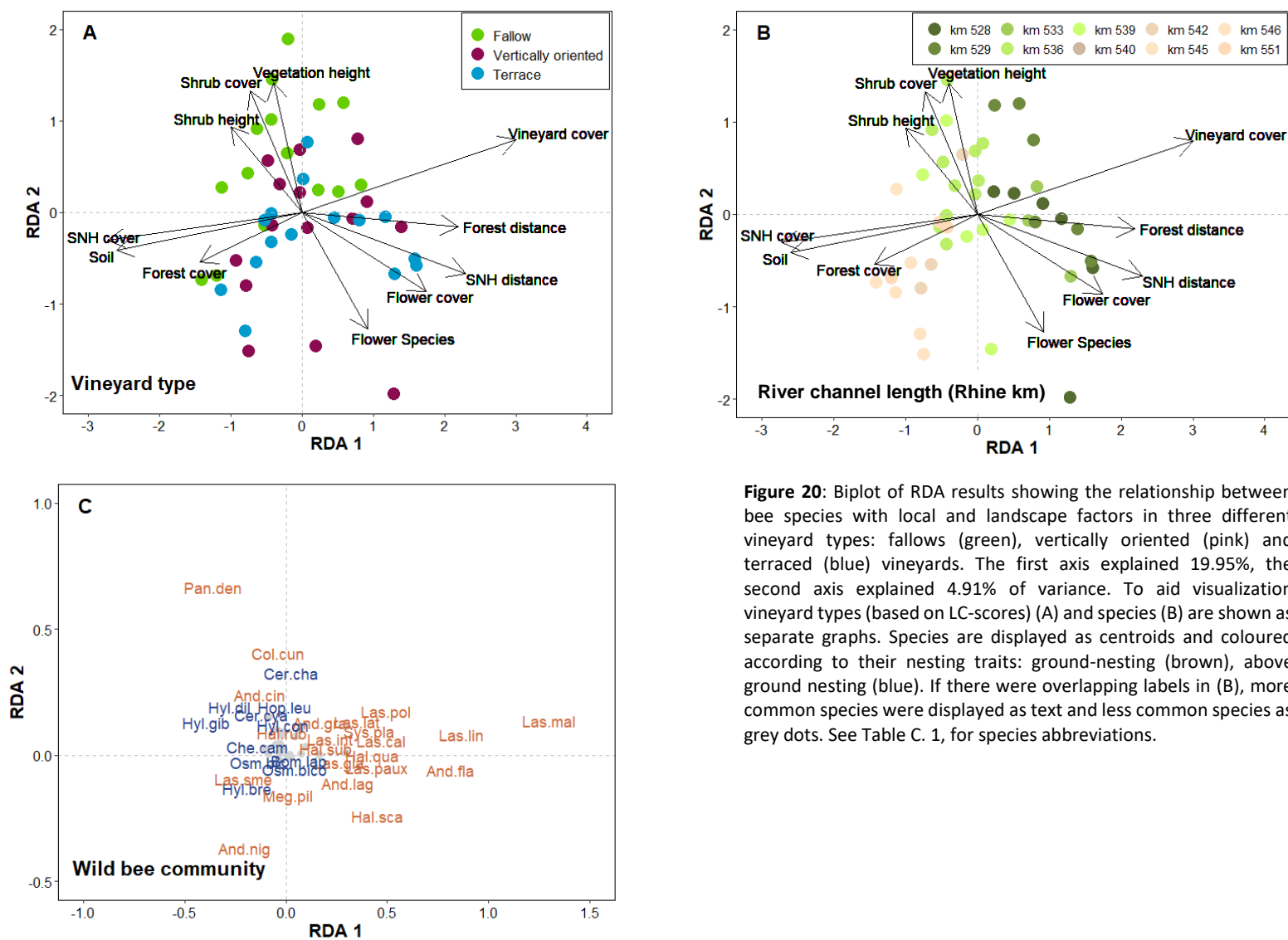


Figure 20: Biplot of RDA results showing the relationship between bee species with local and landscape factors in three different vineyard types: fallows (green), vertically oriented (pink) and terraced (blue) vineyards. The first axis explained 19.95%, the second axis explained 4.91% of variance. To aid visualization vineyard types (based on LC-scores) (A) and species (B) are shown as separate graphs. Species are displayed as centroids and coloured according to their nesting traits: ground-nesting (brown), above ground nesting (blue). If there were overlapping labels in (B), more common species were displayed as text and less common species as grey dots. See Table C. 1, for species abbreviations.

5. Contrasting effects of vineyard type, soil and landscape factors on ground- versus above-ground nesting bees

5.5 Discussion

We found that opposing needs of ground- and above-ground nesting wild bees drive their response to management, local conditions, and landscape factors in a small-structured viticultural landscape, habitat demands that are, until now, most commonly not met by wild bee conservation practices. We argue for a more distinctive and trait-based approach that equally considers the provision of floral and diversified nesting resources as undifferentiated 'one-size-fits-all' approaches are at risk of only restoring one dimension of a species' need, while other factors critical to their survival are neglected. We considered soil composition as a gradient from fine to gravel particles to explain wild bee response in an agricultural setting and found that nesting preferences of ground-nesting bees were determined by soil gravel while above-ground-nesting bees remained unaffected but positively responded to shrub encroachment due to vineyard abandonment.

The small and heterogeneously structured landscape in the UMRV supported a diverse and species-rich wild bee community ($\approx 20\%$ of Germany's wild bee species). Besides species of open habitats, we found many threatened and thermophilic species associated with vineyards such as *Panurgus dentipes* (Westrich 2019) as well as highly specialized species in terms of nesting (e.g., snail-shell nesting *Osmia bicolor*) or foraging (e.g. monolectic *Systropha planidens*) in relatively high abundances. The small structured setting might be the reason, why we did not find huge differences in the overall wild bee richness between the vineyard types besides wild bee species richness, which was higher in fallows than managed vineyards. This was even more pronounced when tested for ground- and above-ground-nesting species separately and is in line with our hypothesis, that specific nesting demands of above-ground-nesting bees are best met by vineyard fallows. At the landscape scale, we found a positive response to an increased cover and proximity of SNH. In our study, most above-ground-nesting bees were cavity-nesters favouring dead wood or hollow plant stems for nesting and profited from pithy stems of *Rubus* species that provide suitable nesting sites for threatened species such as *Ceratina chalybea* (Westrich 2019). SNH such as hedges and other woody habitat structures further provide diversified, natural nesting resources, significant for cavity-nesting bee survival (Drossart and Gérard 2020) alongside the high availability of floral resources (Eckerter et al. 2022). As such, colonization rates (Bihaly et al. 2021) and community diversity (Sheffield et al. 2008) of cavity-nesting bees are higher in adjacent SNHs compared to those in apple orchards. Accordingly, man-made nest constructions only benefit a small proportion of common, widespread species (Rahimi et al. 2021; Fortel et al. 2016).

In addition, woody vegetation can provide valuable floral resources different from sown and spontaneous herbaceous vegetation with regard to plant composition and flower timing (Königslöw et al. 2021; Rollin et al. 2019). Especially in early spring, mass flowering of woody plants such as hawthorn

5. Contrasting effects of vineyard type, soil and landscape factors on ground- versus above-ground nesting bees

is an important nectar and pollen source when floral resources in vineyards are scarce (Bertrand et al. 2019; Garratt et al. 2017). Furthermore, woody vegetation provides important non-floral resources such as resins, leaf pieces, plant sap, and floral petals for nest construction, particularly within cavity-nesting *Megachilidae*, and plays a crucial but often neglected role in wild bee fitness and survival (Requier and Leonhardt 2020). The overall high bee species richness in fallows (Figure C. 4) and positive response to SNH cover in the landscape indicate that ground-nesting species also profited from fallows as partial foraging habitat and emphasize the high ecological value of woody structures for foraging, nesting, and the provision of non-floral resources in agricultural settings. For the majority of ground-nesting species, the nesting biology and variables influencing their nesting behaviour remain largely unknown (Antoine and Forrest 2021; Harmon-Threatt 2020), even though this group comprises approximately 70 % of all bee species (Westrich 2019). Ground-nesting seems to be a defining quality of open-adapted bees (Harrison et al. 2018) which profit from structurally open forms of agriculture such as annual crops and pasture (Brown et al. 2020; Hall et al. 2019; Carrié et al. 2018). We also found ground-nesting bees positively responding to a higher proportion of vineyards in the surrounding landscape, which was associated with a higher amount of bare ground and flower cover compared to fallows. As it is often assumed that ground-nesting bees prefer bare ground or at least sparsely vegetated patches as nesting sites (Carrié et al. 2018; Cane 1997; Potts and Willmer 1997). Kratschmer et al. (2018) suspected that ground-nesting bees profited from undisturbed bare soil patches in vineyard inter-rows. However, we did not find a direct positive effect of higher bare ground availability on species richness or abundance of ground-nesting bees in managed vineyards. Decreasing vineyard area was intermingled with increasing shrub encroachment and altering soil composition that changed from fine and loamy to coarse and schistose soils alongside the river current because wine growing on schistose soils is less productive, less profitable, and is, therefore, more affected by abandonment. Hence, we suggest that in our study area, the association of ground-nesting bees with increasing vineyard area is not only a response to open habitat structures but also an effect of species preferences for certain soil characteristics for nesting.

Abiotic, soil-based variables such as texture (Cane 1991), soil compaction (Sardiñas and Kremen 2014), slope (Carrié et al. 2018; Potts and Willmer 1997), and soil temperature have been discussed to influence nest-site selection. As for ground-nesting females, nest excavation means a major investment of time and energy, they are likely to choose soils where the cost of digging is relatively low (Potts and Willmer 1997). For example, a preference for sandy or sandy loam soils (Cane 1991) might be due to better drainage and facilitate nest excavation (Antoine and Forrest 2021). However, there is great variation among species and more compact soils might provide higher structural integrity and prevent

5. Contrasting effects of vineyard type, soil and landscape factors on ground- versus above-ground nesting bees

nest collapses, which is especially important for social species that nest in aggregations (Antoine and Forrest 2021). We found higher abundances of ground-nesting bees in soils with finer loam particles compared to schistose soils which could be explained by the abrasive nature of coarse particles that are likely to harm and wear mandibles and wings, hamper digging, and reduce nest stability. The latter might be particularly important for the abundant *Lasioglossum* group in our study that build burrows in social aggregations (Westrich 2019) such as *L. malachurum* (12.1% of all individuals) who prefer compact soils with low stone coverage (Polidori et al. 2010). However, it is important to consider that other arthropods may have conflicting needs. For example, endangered species from other groups, such as apollo butterflies or band-winged grasshoppers do benefit from vegetation-free slate soils.

For the slope aspect, it is difficult to distinguish whether bees select sites solely based on the slope or the interplay of slope, aspect, solar radiation, and temperature (Antoine and Forrest 2021). In general, nest temperature is important as it determines the rates of egg and larval development (Sardiñas and Kremen 2014) and the timing of adult emergence (Forrest 2017). Nevertheless, we did not observe a preference of ground-nesting bees for steep terrace embankments where temperatures are likely highest. However, as our study was conducted in a river valley on steep slopes and wine growing is generally restricted to climates of dry and warm summers these variables might be more selective on flat sites (Carrié et al. 2018; Hopfenmüller et al. 2014).

Flower-rich inter-row vegetation has been shown to benefit wild bee abundance and species richness (Peris-Felipo et al. 2021; Kratschmer et al. 2019; Kratschmer et al. 2018). In addition, low-intensity management and the adoption of alternate mowing or tillage have recently been shown to benefit biodiversity and ecosystem services in vineyards (Brambilla and Gatti 2022). Overall bee and ground-nesting bee abundance positively responded to a higher flower cover but this however did not translate into higher bee abundance in managed vineyards. Flower cover was lower in coarse, and schistose soils because growing conditions for plants are more challenging at these sites due to extreme drought and heat. Accordingly, the positive response to flower cover seems interrelated with lower abundances of ground-nesting bees in schistose soils and therefore needs to be interpreted cautiously. In addition, floral resources do not seem limited in the less intensified surrounding of the study area which is rich in semi-natural habitats in the surrounding compared to other agricultural areas.

5.6 Conclusion

Viticulture is one of the few crops that profit from climate change in a way that milder climates allow wine cultivation to expand across many regions at higher elevations or latitudes (Hannah et al. 2013). However, wine growing demands intensive management, particularly on flat terrains, and often leads to fairly featureless and homogeneous landscapes. Therefore, there is a need for diversification of

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vineyard landscapes for biodiversity conservation. In addition to the implementation of strategies such as alternate management or less intense soil and vegetation management that support a broad range of arthropods in vineyards, particular trait-based views within species groups seem mandatory to design more targeted and effective conservation measures. For instance, in our study, above-ground nesting species were relatively low in abundance and had little influence on general community patterns. Consequently, drawing conclusions and giving recommendations on landscape composition from overall abundance would have been misleading as patterns were masked by more abundant ground-nesting species.

For bee conservation in vineyards, heterogeneous landscapes composed of actively managed vineyards and natural elements that complementary provide both floral and nesting resources are critical to fulfilling the many specific needs. For ground-nesting bees, maintaining unpaved roads on loess sites, creating scraped bare ground plots on field edges or artificial nesting hills in addition to establishing woody structures such as hedges for above-ground nesting species should be implemented in bee conservation actions. Especially in simplified vineyard landscapes, farmers should be encouraged to maintain and establish woody elements as they are highly valuable resource providers for both groups. Additionally, when analyzing wild bee response within the landscape context we recommend not only considering landscape structure and composition but also geological and soil parameters as they were particularly important for ground-nesting bees and may influence the success of conservation measures in different regions.

Further, our results emphasize the significance of conserving heterogeneous cultural landscapes to maintain diverse wild bee communities but also to transfer knowledge gained from these valuable habitats to target conservation measures for more intensified agricultural landscapes.

6. Maintaining steep slope viticulture for spider diversity



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Authorship contribution:

VW: Conceptualization, Data curation, Data analysis, Investigation, Methodology, Visualization, Writing - original draft, Writing - review & editing. **SK:** Species identification, Writing - review & editing. **MHE:** Supervision, Writing - review & editing. **IL:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing - review & editing.

6.1 Abstract

Many species-rich ecosystems are threatened by the abandonment or change of commonly-used agricultural practices. Steep slope viticulture, a traditional land use type of important cultural landscapes in Germany, declined strongly in recent decades due to insufficient profitability. The change of cultivation type from vertically planted to modern terraced vineyards may help to reduce the further abandonment of viticulture in these exceptionally species-rich landscapes by keeping management economically viable. However, little is known about the effects of a change in vineyard management type on biodiversity. We determined the effects of vineyard management types (terraced vs. vertically planted) in contrast to vineyard fallows, local habitat characteristics and the surrounding landscape on ground-dwelling spiders (Arachnida: Araneae) in 45 study sites along the Upper Middle Rhine Valley in Germany. A diverse landscape mosaic of vineyard fallows, forests and vineyards created heterogeneity and contributed to a high species diversity irrespective of the vineyard type. Vineyard fallows supported highly distinct spider communities, including some late-successional species, whereas on managed sites and terraced vineyards in particular, many xerophilic species, which are adapted to open habitat structures, prevailed. We conclude that management in steep slope viticulture is crucial to maintain open habitat structures and conserving associated spider species. Likewise, preserving vineyard fallows and overall landscape heterogeneity remains important to maintaining beta diversity and a large species pool.

6.2 Introduction

Landscape simplification and habitat loss caused by agricultural intensification have severe impacts on biodiversity (Díaz et al. 2019; Foley et al. 2005; Benton et al. 2003). Many species have become rare and endangered due to homogenization of once highly structured landscapes (Cardoso et al. 2020; Sánchez-Bayo and Wyckhuys 2019; Benton et al. 2003). In Europe, many cropland species have evolved with traditional agricultural practices and rely on cultivation (Batáry et al. 2015; Sutcliffe et al. 2015) therefore, these species are threatened by the abandonment of traditional agriculture. Thus, conservation of agrobiodiversity will largely depend on the provision of wildlife-friendly land use practices and suitable seminatural habitats (hereafter SNH) within the agricultural landscape (Samways et al 2020; Habel et al 2019; Tscharntke et al 2012).

The cultivation of wine grapes is among the oldest forms of agriculture covering 7.6 million hectares worldwide (OIV 2018). Even though vineyards typically demand intensive management, they can support numerous additional plant (Nascimbene et al. 2013) and arthropod species (Carlos et al. 2019; James et al. 2015; Isaia et al. 2006). In Germany, steep slope viticulture has shaped the appearance, biodiversity and cultural traditions of entire landscapes such as the Upper Middle Rhine Valley (UMRV). Over the last century, this unique kind of agroecosystem faced intense transformation. Traditional cultivation of grape vines on small terraces made of dry stone walls created a structured landscape mosaic that harboured a high degree of xerothermophilic flora and fauna (Kratschmer et al. 2018; Petit et al. 2012; Boller et al. 1997). To enhance productivity, vineyards were planted in a downhill direction on steep slopes (“vertical orientation” hereafter, see Figure 21), thus increasing mechanisation as well as the area under cultivation. Viticultural intensification resulted in the removal of dry-stone walls and natural landscape elements such as trees and grassy margins, thus reducing small-scale heterogeneity. Nevertheless, growing grapevines on steep slope sites still requires substantial manual work (Strub et al. 2021). In recent years, steep slope vineyards have increasingly been abandoned due to insufficient profitability, thereby causing an increase in the area of fallow land (up to 39% in the Middle-Rhine Valley; 1987 – 2019)(Stoll and Schultz 2020). Vineyard fallows can potentially act as islands in an intensively used agricultural landscape by providing diverse microhabitats (Duelli and Obrist 2003); however, the appropriate management required to preserve open habitat structures is often lacking (Veith et al. 2012). Consequently, progressive succession is causing the flora and fauna of non-forest open habitats to disappear from abandoned vineyards.

One approach to keep management economically viable and thereby halt the decline of viticulture on steep slopes is modern vineyard terracing. In this approach, vineyard rows run parallel to the hillside, thus facilitating management and lowering production costs (see Figure 21). Because a large proportion of European biodiversity today depends on habitat provision through extensive farming practices

(Sutcliffe et al. 2015), there is a call for coupling conservation measures and yield production in an integrated matrix of natural habitats and crops (Grass et al. 2019). Terraced vineyards could serve these needs as they create habitat heterogeneity within the agricultural system. A substantial area of terraced vineyards is composed of embankments that remain uncultivated, thus terraced vineyards could profitably combine winegrowing and conservation in a land-sharing approach. In terms of conservation, terrace embankments can be of high value for xerothermophilic communities due to their thermal potential and low disturbance level (Košulič et al. 2014).

Spiders are a highly diverse and abundant group of arthropod predators in most terrestrial ecosystems (Wise 1993). They often occur in high numbers in agricultural landscapes and greatly contribute to pest control (Michalko et al. 2019). Species occurrence is related not only to microhabitat conditions such as vegetation structure (Bonte et al. 2002), bare soil patches, disturbance and management regime (Hamřík and Košulič 2021; Marc et al. 1999) but also to landscape complexity (Rosas-Ramos et al. 2018; Schmidt et al. 2005). Similar to other invertebrates, spiders show long-term population declines. In Germany, about 40 % of spider species decreased in abundance over recent decades (Blick et al. 2016).

Vineyards have been shown to provide a rather stable habitat for spiders and can host high spider diversity, including a considerable number of threatened species (Košulič et al. 2014; Isaia et al. 2006). Spider species richness and abundance in vineyards are positively affected by natural elements such as SNHs, hedges and forests in the vicinity of vineyards (Gaigher and Samways 2014; Prieto-Benítez and Méndez 2011). Although effects of organic versus conventional management (Kolb et al. 2020; Caprio et al. 2015; Gaigher and Samways 2014) and soil disturbance intensity (tillage, mowing) (Pfungstmann et al. 2019; Bruggisser et al. 2010), have already been studied, less is known about the potential of vineyard terraces for spider biodiversity. Previous surveys have concentrated on either comparing species assemblages of terraced vineyards with those of SNHs (Carlos et al. 2019) or simply describing spider diversity of vineyard terraces (Košulič et al. 2014). To our knowledge, studies that focussed on the value of steep slope viticulture in contrast to vineyard fallows for spider diversity do not exist. Further, the effects of various management systems in steep slope viticulture on spider diversity have not yet been studied. Such a study may also be valuable in guiding farmland conservation efforts on steep slope vineyards.

The aims of this study were to assess the significance of steep slope viticulture for spiders by comparing the conservation value of terraced vineyards, vertically oriented vineyards and vineyard fallows. We asked whether (1) the different structure of vineyard types in contrast to fallows affects spider diversity, abundance, predatory guilds and habitat preferences of spiders, if (2) spider communities differ among

vineyard types in contrast to fallows and (3) what influence local vineyard and landscape parameters have on spider species richness, abundance, predatory guilds and community composition.

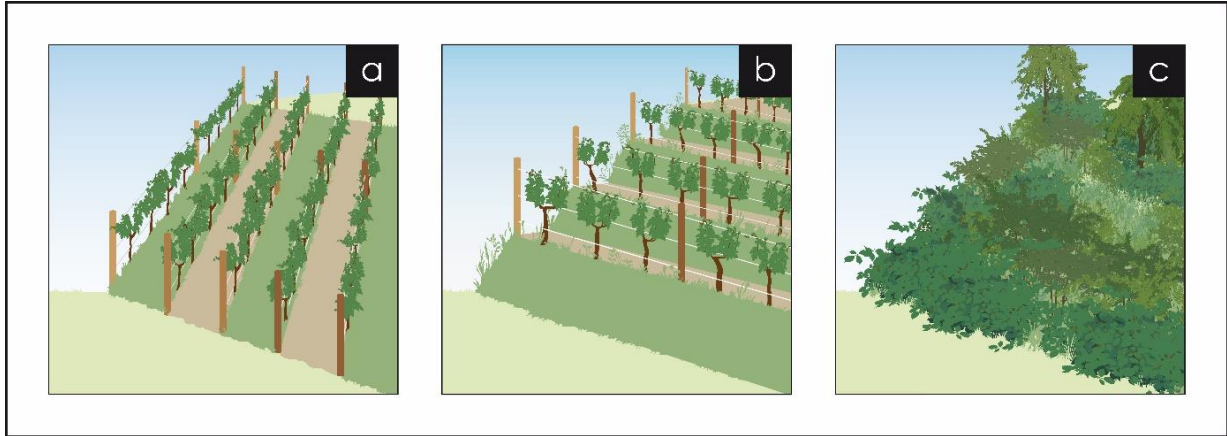


Figure 21: Three vineyard types were studied: vineyards with vertically oriented rows (a), terraced vineyards (b) and vineyard fallows (c). Vertically oriented vineyards usually received an alternating tillage treatment, i.e. every second inter-row was tilled while the other was permanently covered with vegetation. Terraced vineyard embankments were detracted from management, permanently covered with vegetation and mown once a year. Inter-rows of terraced vineyards were tilled. Vineyard fallows were not managed and abandoned for at least 10 years.

6.3 Material and Methods

6.3.1 Study sites

The study was conducted in the wine-growing region of the UMRV in Hesse (50.042342°N, 7.814533°E) and Rhineland-Palatinate (50.119139°N, 7.719275°E), Germany (see Figure 22 for details). The climate is sub Atlantic with an annual mean temperature of 11.6 °C and total annual precipitation of 554 mm (Lorch, 2015-2019, weather station Hochschule Geisenheim). All sampling sites had clayey loam, clay or loess soils as the prevailing soil texture, partially including limestone. Three sites had slate soils.

We sampled 15 vineyard triplets, each including a terraced vineyard, a vineyard with vertically oriented rows and a vineyard fallow for a total of 45 study sites (hereafter summarized as vineyard types, see Figure 21 for details). Within triplets, study sites were selected to be in close vicinity to each other in order to achieve similar environmental conditions. The vineyards were provided by 14 winegrowers and managed according to the standards of integrated pest management (EU Directive 2009/128/EC). Based on the plant protection schemes for the vegetation period of 2018 and 2019, we measured the total number of pesticide treatments (as the number of spraying events applying one or more substances). Pesticides encompassed fungicides and herbicides; insecticides were not applied. Grape variety, age of grapevines, size of vineyard and orientation differed among sites. Inclination ranged from 17° to 42°. Most of the vertically oriented vineyards (12) received an alternating tillage treatment, i.e. every second inter-row was tilled at least once a year while the other inter-row was not tilled, but permanently covered with vegetation. The vineyards with slate soils were not tilled (3). All inter-rows of the terraced vineyards were tilled at least once a year. Terrace embankments were permanently

covered with vegetation and usually mown once a year. Vineyard fallows were abandoned for at least 10 years and showed different stages of succession. Most fallows were overgrown with shrubby vegetation dominated by blackberry (*Rubus fruticosus* agg.), dog rose (*Rosa canina* agg.), wild cherry (*Prunus avium* (L.) L.) or midland hawthorn (*Crataegus laevigata* (Poir.) DC., s. l.).

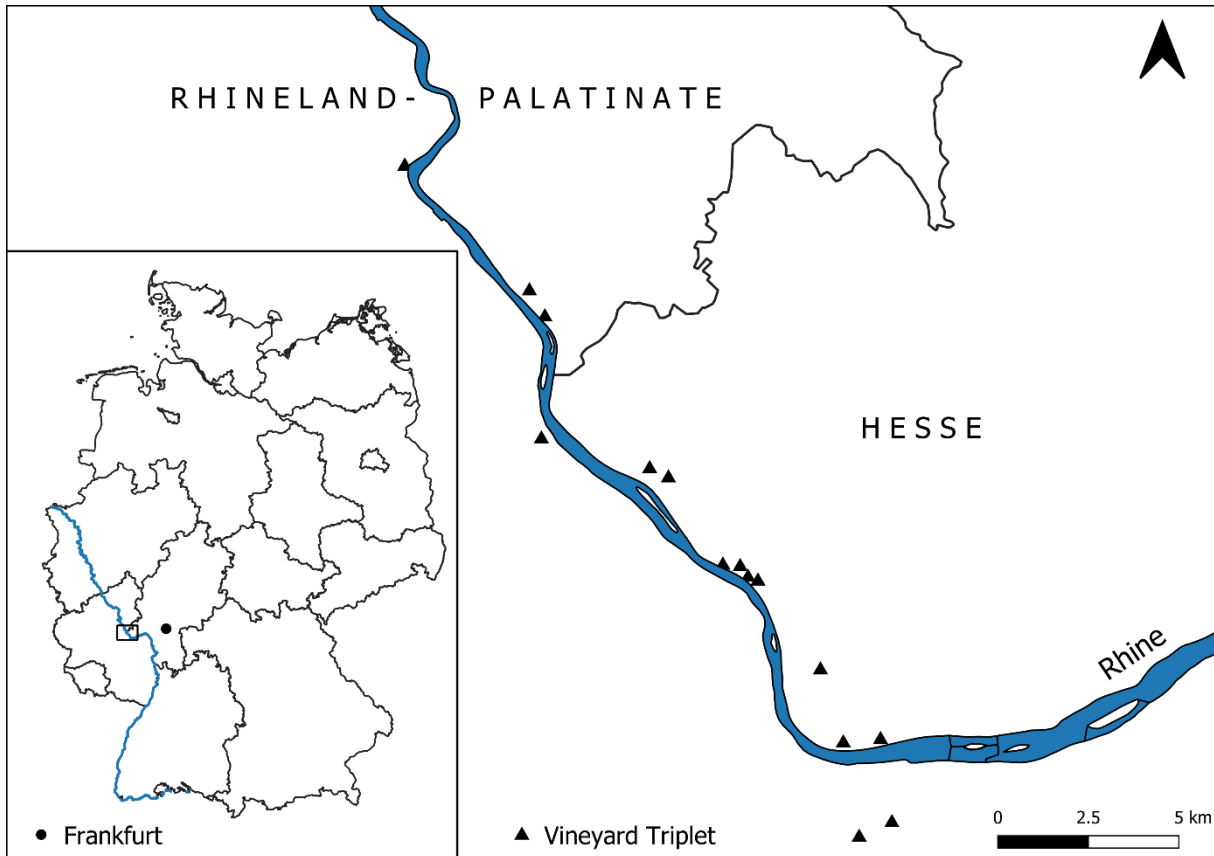


Figure 22: Location of study sites in the German winegrowing region of the Upper Middle Rhine Valley. 15 triplets of adjacent vertically oriented vineyards, terraced vineyards and vineyard fallows were selected.

6.3.2 Spider sampling

We used pitfall traps for spider sampling that were embedded in the soil up to the rim. Traps consisted of transparent polypropylene cups (200 ml, 6.8 cm diameter, 9.8 cm height) and were filled $\frac{2}{3}$ with trapping solution (25% propylene glycol with a few drops of odour-free detergent as surfactant). In each study site, three pitfall traps were placed 5 m apart along a transect in the centre of the vineyard. For each terraced vineyard, one trap was placed in the embankment, one in an inter-row and one beneath the grapevines. For the vertically oriented rows, two of the traps were placed in adjacent inter-rows, the third beneath the grapevines. For the fallows, the traps were evenly distributed over the site. Sampling took place in two consecutive years with two sampling periods of 9 days each (May/August 2018, May/September 2019). Weather conditions were similar among sampling periods and years. All spiders were stored in Scherpeltz-solution (70 % Ethanol, 25% distilled water, 5% glacial acetic acid) and identified to species level with determination keys (Nentwig et al. 2019; Roberts 1987, 1995) and

nomenclature following World Spider Catalog Version 22.0 (World Spider Catalog 2020). Adult spiders were identified to species and immatures to family or genus level. Additionally, the number of ant individuals (adults and juveniles) per trap was counted.

6.3.3 Environmental variables

Local vegetation parameters were recorded around each trap position in two plots in rectangles of 0.5 × 2 m for managed vineyards and rectangles of 1 × 1 m for fallows (6 plots per site). Within each plot, we visually estimated the cover of bare ground, litter, herbaceous vegetation, shrubs and trees as a percentage proportion and measured the height of vegetation and shrubs (five random measurements). All subplots were sampled twice during the growing season (May/August 2018, May/September 2019). Mean values were calculated and averaged over the four sampling periods. Soil was classified along a gradient from fine to coarse soil particles by visually estimating the proportion and size of fine (< 2 mm) and coarse soil particles in a rectangle of 0.4 × 0.4 m. Coarse soil particles were subdivided into three groups according to their size: < 1 cm, 1 - 4 cm and > 5 cm.

6.3.4 Landscape analysis

For analyses of the landscape around study sites, we calculated the cover of semi-natural habitats, forests and vineyards within a radius of 150 m centred in the sampling plot. This radius was chosen to cover the slope range on which vines are cultivated without including the Rhine. SNH elements encompassed woody habitats such as vineyard fallows, hedgerows and herbaceous habitats. As a reference, we used the digital landscape model for Germany from 2009 (DLM-DE 2009), which we matched and updated with orthophotos (resolution of 40 x 40 cm) provided by the Hessian State Office of Land Management and the Surveying and Geographic Information Office Rhineland-Palatinate. The analysis was carried out using ArcGIS 10.7.1 (ESRI 2019). Additionally, we measured the distance from the centre position of each trap to the closest SNH and forest using Google Earth Pro (Google Earth 2020).

6.3.5 Data Analysis

For all analyses, the R software (R Core Team 2020) was used. Figures were created with ggplot2 (Wickham 2016), cowplot (Wilke 2019), QGIS (QGIS Development Team 2019) and Adobe Illustrator (Adobe 2012).

All samples per site were pooled over the four sampling periods and two sampling years (12 traps) because catches showed similar patterns among sampling periods and years. For species-level analyses such as species richness and community composition, only adult individuals were included, as reliable identification to species level is not always possible for immature specimens. Females of *Pardosa saltans* (Töpfer-Hofmann, 2000) and *P. alacris* (C. L. Koch, 1833) (39 ind.) were omitted from species analysis because they could not be assigned reliably to one of the two species and readily

distinguishable males were present in high numbers. Abundances and species richness were extrapolated for traps that were lost during sampling (7 traps in fallows, 4 in vertically oriented, 1 in terrace vineyards). A detailed description of trap extrapolation is given in Kolb et al. (2020).

According to Cardoso et al. (2011), we assigned spiders to eight predatory guilds that have specific foraging strategies to catch their prey: ambush hunters, ground hunters, other hunters (typically hunting on vegetation), orb web weavers, sensing web weavers, sheet web weavers, space web weavers and specialists (selecting a narrow range of prey types). We assumed ground hunters to be better represented by pitfall trapping than other guilds. To account for this bias, we only considered ground hunters for the model selection of local and landscape parameters. Indicator species for each vineyard type were generated using the IndVal procedure (Dufrêne and Legendre 1997), which is obtained as the product of the probability of a site being associated with a site-group combination where the species has been found and the probability of finding that species at a site associated to that group (function “multipatt”, package *indicpecies*; (Cáceres and Legendre 2009)). P-values were obtained using a permutation test with 9999 permutations. To distinguish widespread from rare species, we approximated species commonness by the number of records for Germany from the Atlas of the European Arachnids (Arachnologische Gesellschaft 2020). The number of records gives the number of recording locations and times disregarding the number of individuals in each record. To consider the current situation, we used all records as from 2000 and calculated a community-weighted mean (CWM) of species commonness per site.

Environmental preferences for spiders were derived from an indirect gradient analysis, in which the composition of central European spider assemblages differentiated along gradients of moisture and shading of the habitat (Entling et al. 2007). For calculation, we used the standard deviation of shading and moisture positions and calculated mean values per site. Values were not available for 21 species because they were absent in the dataset from Entling et al. (2007).

We chose (generalized) linear mixed effect models (GLMMs) with following post-hoc tests to analyze differences between vineyard types on spider abundances, species richness, the commonness of species, positions of shading and moisture and environmental parameters (function “glmmTMB”, package *glmmTMB*; (Brooks et al 2017)). Post-hoc-tests were applied using the *emmeans* package (Lenth 2020). Vineyard triplet (factor with 15 levels) was added as random effect to each model, except for the model containing the spraying events, where “winegrower” was used as a random factor. Data exploration was conducted according to the protocol of Zuur et al. (2010). Vineyard type was used as categorical variable (fallow/terrace/vertically oriented). Fallow was used as a baseline for parameter estimation in the models. For count data, we used Poisson distribution. If overdispersion was detected,

we used negative binomial, or in the case of underdispersion, Conway-Maxwell-distribution was used. For continuous data, Gaussian distribution was used. For use as a response variable, the local vegetation parameters, vegetation cover and height, were log-transformed and shrub cover and shrub height were square-root transformed to reduce skewness.

To identify drivers of spider and ground hunter species richness and abundance, we choose manual stepwise model selection of appropriate GLMMs via the AICc-criterion. Before model building, the explanatory variable set was reduced using a PCA and by excluding variables with a variance inflation factor (VIF) > 2. Initially, the set encompassed all local vegetation parameters (vegetation height, shrub height, bare ground cover, litter cover, vegetation cover, shrub cover, tree cover and soil), all landscape variables (SNH%, forest%, distance to SNH, distance to forest) and the vineyard types (fallow/terrace/vertically oriented). The final variable set was reduced to vegetation cover, soil, SNH%, distance to forest and vineyard type. Vineyard triplet was used as a random factor. For each response variable, the appropriate distribution was chosen depending on the variable type and adjustment for under- or overdispersion as described above. Numerical explanatory variables were scaled and centred before testing. Model selections were done manually via the Akaike information criterion for small sample sizes (AIC_c) using the drop1-function (package: MuMIn; Barton 2020). Conditional and marginal R²s were calculated (package: sjstats; Lüdecke 2020).

Differences in spider communities in relation to vineyard type and environmental and landscape parameters were analysed using the vegan package (Oksanen et al. 2020). We performed a Detrended Correspondence Analysis (DCA) and considered the length of gradient as a measure of the species turnover (Lepš and Šmilauer 2010). The lengths of gradient of 2.42 (1st axis) and 2.18 (2nd axis) indicated that a linear model was more appropriate, so a Principal Component Analysis (PCA) was conducted. Landscape and local vegetation parameters that were significantly related to the PCA axes (< 0.05, based on a permutation test with 9999 permutations) were included post-hoc by projection. To reduce the influence of dominant species, we log₁₀ (x + 1) transformed the community data and excluded species with less than three occurrences from the analysis, thus reducing the number of species from 119 to 54 in total. All environmental and landscape variables were standardized to zero mean and unit variance before the analysis (function “scale”, package: vegan).

6.4 Results

In total, we sampled 5496 spiders, of which 73.52 % were adult individuals. The spider community was comprised of 121 species from 25 families. The most abundant spider species were the ant-eating spider *Zodarion italicum* (Canestrini, 1868) (26.28 % of adult individuals), *Aulonia albimana* (Walckenaer, 1805) (15.24 %) and *Titanoeca quadriguttata* (Hahn, 1833) (5.54 %). We collected 17

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species of conservation concern, which are listed on the Red List of spiders in Germany (Blick et al. 2016) (Table D. 1). The predatory guild of ground hunters had the highest species richness and abundance (Table 10). Diet specialists encompassed only 6 species, yet 27.53 % of all individuals belonged to this guild due to the high abundance of *Z. italicum*. To account for the food availability of *Z. italicum*, we evaluated the ant (Hymenoptera: Formicidae) bycatch of the pitfall traps. In total, 18.017 ant individuals were found, showing a significantly higher abundance in managed vineyards than in fallows (Figure D. 1).

6.4.1 Differences between vineyard types

6.4.1.1 Environmental variables

Local vegetation parameters differed significantly between vineyard types (Table 9), but the foremost differences were found between both managed vineyard types and fallows. On average, fallows showed increased vegetation and shrub height and shrub cover as well as up to 52 % higher litter cover. Trees were only present in fallows. Bare ground cover was nearly three times higher in managed vineyards than in fallows. The number of spraying events did not differ significantly between vertically oriented and terraced vineyards and had no significant effect on spider species richness and abundance.

Table 9: Effects of vineyard type on local vegetation parameters and number of spraying events (N = 15). (G)LMMs were used with vineyard triplet as a random factor for vegetation parameters and winegrower as a random factor for number of spraying events. Different letters indicate significant differences between vineyard types ($p < 0.05$).

Variable	Vertically oriented	Terrace	Fallow
Vegetation height ^x [cm]	16.24 ^a ± 1.06	19.81 ^a ± 0.82	48.15 ^a ± 5.01
Shrub height ^{xx} [cm]	0.00 ^c ± 0.00	0.90 ^b ± 0.38	104.82 ^a ± 11.81
Bare ground cover [%]	63.93 ^a ± 3.09	61.87 ^a ± 4.72	23.60 ^b ± 3.85
Litter cover [%]	19.67 ^{ab} ± 2.17	15.20 ^b ± 1.85	23.07 ^a ± 3.17
Vegetation cover ^x [%]	26.53 ± 3.29	28.00 ± 2.55	26.53 ± 3.51
Shrub cover ^{xx} [%]	0.40 ^c ± 0.40	2.13 ^b ± 0.77	38.87 ^a ± 6.57
Tree cover [%]	0.00 ± 0.00	0.00 ± 0.00	9.87 ± 4.23
Nr. of spraying events	7.63 ± 0.41	6.77 ± 0.47	-

^x Square-root transformed data were used for testing

^{xx} Log-transformed data were used for testing

6.4.1.2 Spider fauna

Spider abundance and spider species richness were not significantly different among the three studied habitat types (Figure 23 A & B). Spider communities in vineyard fallows were composed of less common species than vertically oriented vineyards with terraced vineyards in between (Figure 23 C). Fallows had substantially more (29) exclusive species than terraced (9) or vertically oriented (6) vineyards (Table D. 2). Together, managed vineyards (N = 30) had 29 exclusive species. Species richness of predatory guilds did not differ significantly between vineyard types (Table 10). Abundance of specialists and space web weavers was significantly lower in fallows compared to terraced and vertically oriented vineyards.

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Ambush hunters were significantly more abundant in fallows than in terraced vineyards, whereas sheet web weaver abundance was significantly highest for vertically oriented vineyards. Indicator species analysis revealed 14 spider species that were significantly associated with one vineyard type (Table 11). Vertically oriented vineyards had more (6) indicator species, than terraced vineyards (3) and fallows (5). In accordance with the community-weighted means, the two rarest indicator species (*Drassyllus villicus* and *Pardosa alacris*) were associated with fallows, while vertically oriented vineyards supported the most common species (*Agyneta rurestris* and *Diplostyla concolor*) (Figure 23, Table 11). Habitat preferences derived from Entling et al. (2007) showed a stronger preference for dry conditions in terraced vineyards than in vertically oriented vineyards or fallows (Figure 23 D). Preference for shaded conditions differed between the three vineyard types, with vertically oriented vineyards having the lowest preference and fallows having the highest (Figure 23 E).

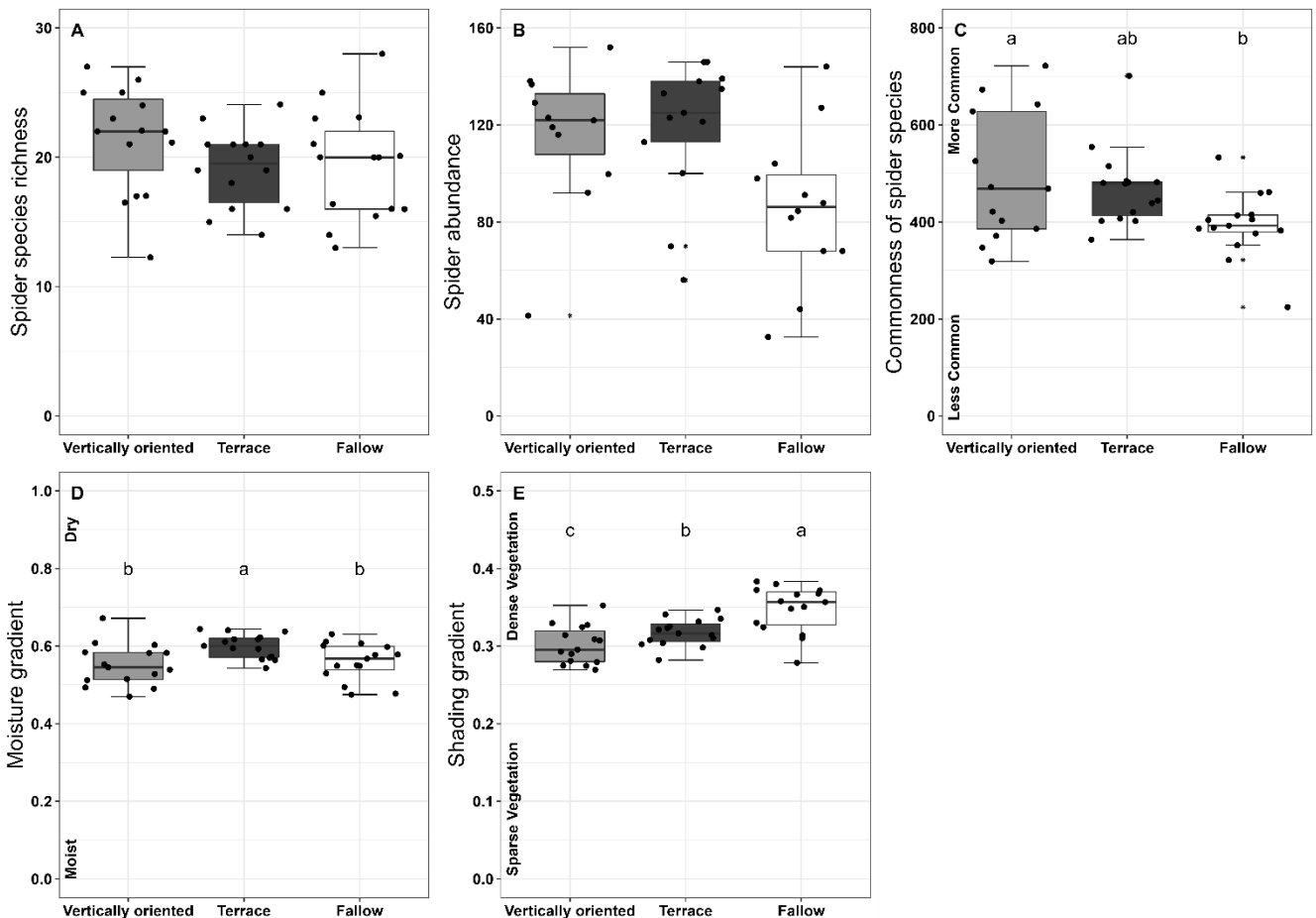


Figure 23: Differences in spider species richness (A), abundance (B), commonness of spider species (C), moisture preference (D) and shading preference (E) between vineyard types analysed using (G)LMMs. Each data point represents the mean number of species or individuals for the respective vineyard type (N = 15). For commonness of spider species points display community-weighted means. Different letters indicate significant differences between vineyard types ($p < 0.05$).

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Table 10: Differences in species richness and abundance for predatory guilds between vineyard types analysed using GLMMs. Means and standard errors per vineyard type are displayed (N = 15). Different letters indicate significant differences between vineyard types ($p < 0.05$).

Predatory guild	Vertically oriented	Terrace	Fallow
Species richness			
Ambush hunters	0.87 ± 0.22	0.60 ± 0.16	1.13 ± 0.22
Ground hunters	12.27 ± 0.90	10.87 ± 0.87	10.67 ± 0.86
Other hunters	1.47 ± 0.27	1.87 ± 0.27	1.67 ± 0.33
Orb web weavers	0.20 ± 0.11	0.13 ± 0.09	0.06 ± 0.06
Sensing web weavers	0.07 ± 0.07	0.00 ± 0.00	0.00 ± 0.00
Sheet web weavers	2.73 ± 0.28	2.67 ± 0.27	2.07 ± 0.38
Space web weavers	1.87 ± 0.27	2.13 ± 0.24	1.67 ± 0.25
Specialists	1.27 ± 0.12	1.47 ± 0.17	1.40 ± 0.19
Abundance			
Ambush hunters	1.33 ^b ± 0.46	0.73 ^b ± 0.21	2.67 ^a ± 0.88
Ground hunters	43.93 ± 6.63	42.27 ± 3.91	51.93 ± 9.95
Other hunters	3.40 ± 1.52	3.20 ± 0.77	2.00 ± 0.44
Orb web weavers	0.20 ± 0.11	0.13 ± 0.09	0.07 ± 0.07
Sensing web weavers	0.07 ± 0.07	0.00 ± 0.00	0.00 ± 0.00
Sheet web weavers	11.33 ^a ± 2.28	6.33 ^{ab} ± 1.17	3.20 ^b ± 0.67
Space web weavers	7.73 ^a ± 1.71	9.93 ^a ± 2.41	2.47 ^b ± 0.45
Specialists	23.53 ^a ± 2.93	34.73 ^a ± 6.43	15.07 ^b ± 3.50

Table 11: Indicator spider species and respective values of species commonness for the three vineyard types. Means and standard errors per vineyard type are displayed (N = 15). Species significantly associated with one vineyard type are printed in bold. Respective p-values are given ($p < 0.05$).

Species	Vertically oriented	Terrace	Fallow	p	Commonness
<i>Agyneta rurestris</i>	8.00 ± 2.35	3.60 ± 1.17	0.00 ± 0.00	0.0008	1954
<i>Argenna subnigra</i>	0.60 ± 0.19	0.20 ± 0.11	0.13 ± 0.13	0.0439	255
<i>Diplostyla concolor</i>	0.40 ± 0.16	0.00 ± 0.00	0.00 ± 0.00	0.0069	1089
<i>Drassyllus villicus</i>	0.47 ± 0.26	1.40 ± 0.47	3.80 ± 1.50	0.0183	48
<i>Ozyptila praticola</i>	0.00 ± 0.00	0.00 ± 0.00	2.00 ± 0.75	0.0001	464
<i>Pardosa agrestis</i>	0.40 ± 0.16	0.00 ± 0.00	0.00 ± 0.00	0.0007	384
<i>Pardosa alacris</i>	0.40 ± 0.27	0.93 ± 0.28	6.27 ± 2.92	0.0008	129
<i>Pardosa hortensis</i>	6.73 ± 1.60	2.80 ± 0.76	2.20 ± 0.73	0.0019	266
<i>Pardosa saltans</i>	0.40 ± 0.19	0.26 ± 0.15	3.60 ± 1.82	0.0042	373
<i>Titanoeca quadriguttata</i>	6.07 ± 1.66	8.00 ± 2.16	0.87 ± 0.29	0.0350	243
<i>Trachyzelotes pedestris</i>	1.00 ± 0.46	1.00 ± 0.40	4.47 ± 0.91	0.0002	218
<i>Xysticus kochi</i>	0.73 ± 0.21	0.33 ± 0.19	0.13 ± 0.09	0.0367	738
<i>Zelotes petrensis</i>	1.40 ± 0.31	3.20 ± 0.62	1.60 ± 0.45	0.0415	415
<i>Zodarion italicum</i>	22.27 ± 3.23	33.80 ± 6.48	14.27 ± 3.54	0.0205	610

6.4.2 Influence of local and landscape parameters

We found multiple effects of local and landscape parameters on spider and ground hunter species richness and abundance (Table 12). Spider and ground hunter species richness significantly decreased along the gradient from fine to coarse soil particles. Ground hunter species richness as well as abundance of spiders and ground hunters was significantly enhanced by higher vegetation cover (Figure 24 A). Spider abundance positively responded to vertically oriented vineyards. A closer distance to forest had a positive effect on ground hunter species richness as well as spider and ground hunter

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abundance (Figure 24 B). An increasing SNH cover in the surrounding landscape significantly decreased the abundance of spiders (Figure 24 C) and ground hunters.

Spider communities were differentiated along the first PCA-Axis between fallows and managed vineyards (Figure 25). The first axis mainly correlated with local vegetation parameters. Fallow sites were associated with higher vegetation and shrub height and shrub and tree cover while managed vineyards showed a positive relationship with high bare ground cover. In spite of clear patterns of the local vegetation parameters, on the landscape scale, only the distance to forest had a significant effect on spider communities.

Table 12: Effects of vineyard type, local vineyard and landscape parameters on species richness and abundance of spiders and the predatory guild of ground hunters. The presented estimates and p-values are obtained from the most parsimonious model after stepwise model selection (full model: $Y \sim \text{Intercept} + \text{vineyard type} + \text{vegetation cover} + \text{distance to forest} + \text{soil} + \text{SNH cover}$ with vineyard triplet as random factor). Marginal R^2 gives explained variation without and conditional R^2 with the random factor. Significant predictors ($p < 0.05$) are printed in bold.

Dependent variable	Predictors	Estimates \pm SE	p-Value	R^2_{marg}	R^2_{cond}	AICc
Spider species richness	(Intercept)	3.10 \pm 0.07	<0.0001	0.21	0.95	249.1
	System vertically oriented	0.09 \pm 0.06	0.1406			
	System terrace	0.02 \pm 0.06	0.7717			
	Vegetation cover	0.05 \pm 0.03	0.0571			
	Soil	-0.05 \pm 0.02	0.0034			
Spider abundance	(Intercept)	4.64 \pm 0.93	<0.0001	0.28	0.45	471.4
	System vertically oriented	0.25 \pm 0.12	0.0429			
	System terrace	0.17 \pm 0.12	0.1690			
	Vegetation cover	0.10 \pm 0.05	0.0383			
	Distance forest	-0.12 \pm 0.06	0.0501			
	SNH %	-0.12 \pm 0.05	0.0454			
Ground hunter species richness	(Intercept)	3.13 \pm 0.30	<0.0001	0.43	0.94	231.0
	Vegetation cover	0.10 \pm 0.04	0.0095			
	Distance forest	-0.14 \pm 0.05	0.0059			
	Soil	-0.09 \pm 0.04	0.0142			
Ground hunter abund	(Intercept)	3.73 \pm 0.74	<0.0001	0.50	0.67	397.9
	Vegetation cover	0.22 \pm 0.07	0.0010			
	Distance forest	-0.40 \pm 0.09	<0.0001			
	SNH%	-0.26 \pm 0.08	0.0009			

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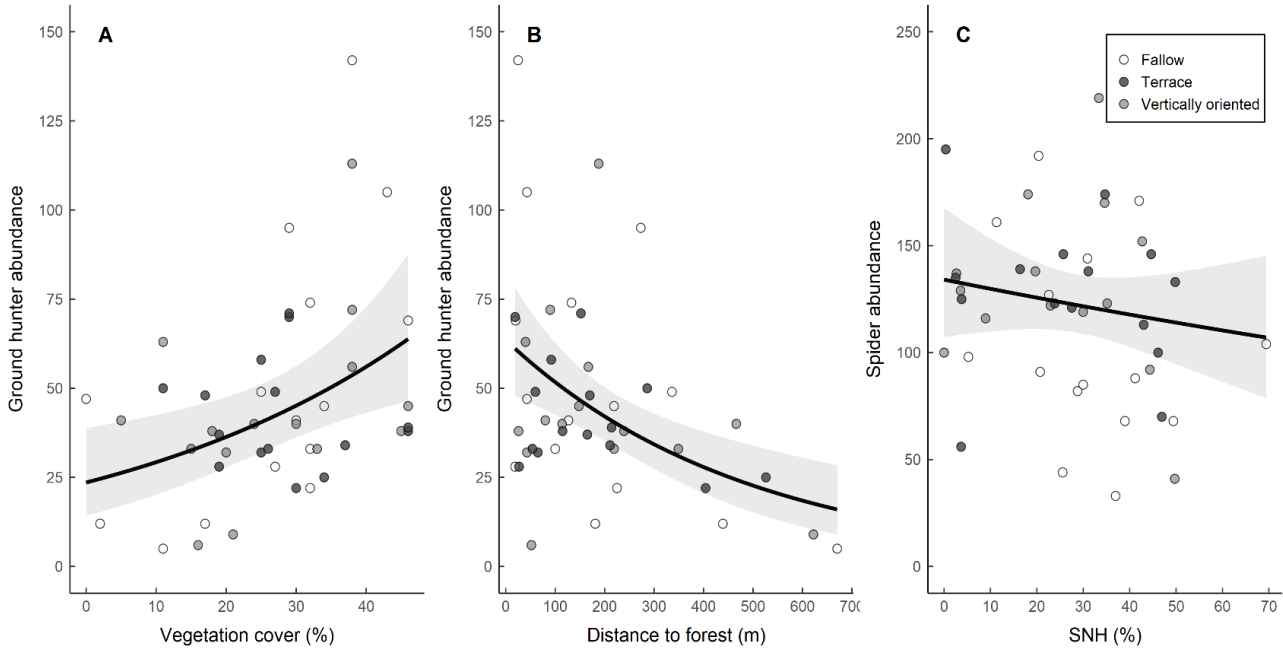


Figure 24: Relationship of ground hunter abundance with vegetation cover and distance to forest and spider abundance with SNH cover within a radius of 150 m. Grey areas represent SE. White dots represent vineyard fallows, dark grey dots represent terraced vineyards and light grey dots represent vertically oriented vineyards respectively. See Table 12 for details.

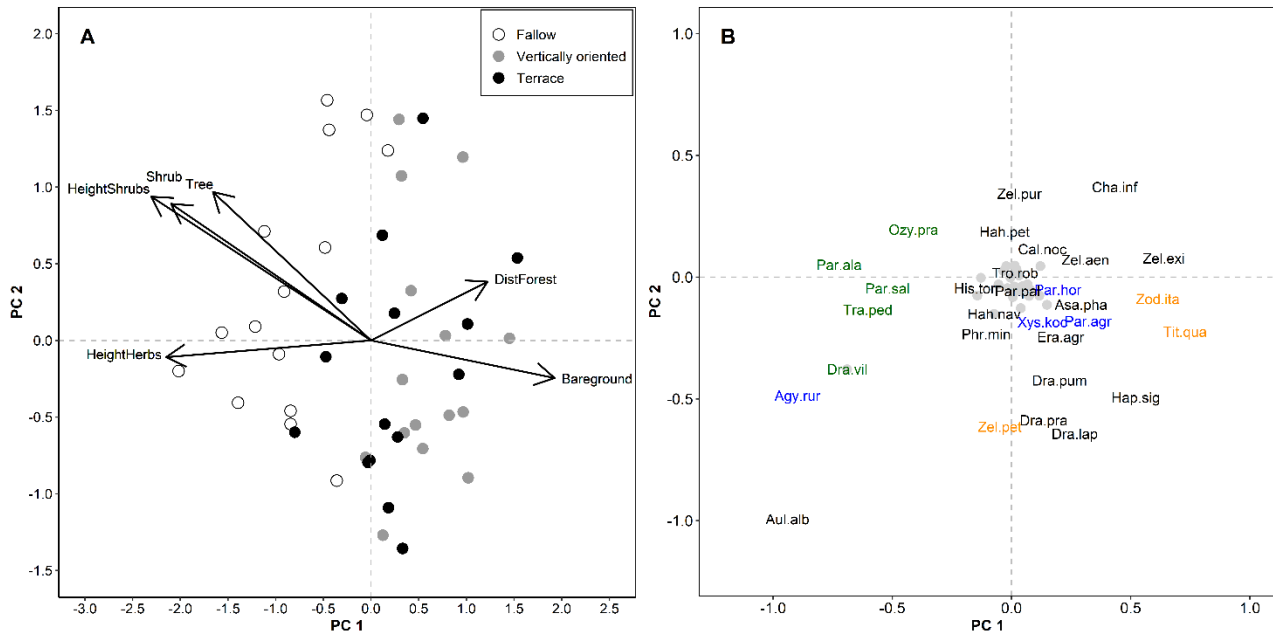


Figure 25: PCA results for spider species composition. The first two components explained 34.5 % of variance. To improve visibility, sites (A) and species (B) are shown as separate graphs. The site plot shows sample scores for fallows (white), vertically oriented (grey), and terraced (black) vineyards. Environmental variables that were significantly related to the PCA axes ($p < 0.05$, 9999 permutations) were included post-hoc by projection. If there were overlapping labels in (B), more common species were displayed as text and less common species as grey dots. Indicator species of vineyard types are coloured in green (fallow), blue (vertically oriented) and yellow (terrace). For black-coloured species names, no assigned indicator values were available. See Table D. 2, supplementary material for species abbreviations.

6.5 Discussion

6.5.1 Spider diversity within the viticultural landscape

The steep-slope viticultural landscape of the UMRV supported high spider diversity and diverse communities for all vineyard types. Comparatively high numbers of rare and threatened species were sampled. This contrasts with results from a similar study in flat terrain vineyards conducted with the same sampling design in the immediate vicinity (Kolb et al. 2020). Twelve threatened species were present in the active vineyards of the current study as compared to only three threatened species in Kolb et al. (2020); nonetheless, overall species richness was similar (UMRV 2018: 77; 2019: 67 versus Rhine-Hesse 2016: 62 species). Irrespective of the management system, the spider community in flat terrain vineyards was strongly dominated by *Pardosa agrestis* (Westring, 1861), an agrobiont species mostly dominant in annual crops, whereas on steep slope sites, this species was hardly present and no other single species had such a high dominance. These considerable differences indicate the great value of viticulture in the UMRV for spider diversity and conservation. However, knowledge of spider diversity in steep slope viticulture is scarce and the effects of vineyard abandonment are poorly studied, which suggests that more research is required.

6.5.2 Factors driving spider diversity within the viticultural landscape

Every vineyard type harboured multiple spider species and produced similar richness values. However, distinct vegetation structures among vineyard types affected spider habitat preferences, predatory guilds and community composition. The transition from herbaceous vegetation in managed vineyards to shrubby vegetation with woody elements in vineyard fallows appeared to be the key determinant of spider community turnover. This is in accordance with Entling et al. (2007), who found that shading was the main driver of community differentiation in Central European spiders. Shading is related to vegetation structure which in our study is affected by distinct management and disturbance intensities. Consequently, unmanaged vineyard fallows were inhabited by more shading-tolerant species and had fewer open habitat specialists. Nevertheless, vineyard fallows supported rare and unique species that were not found in managed vineyards and, thus, contributed significantly to the overall diversity. Contrary to fallows, vertically oriented vineyards hosted more common species that were mostly associated with open and ruderal areas. However, in contrast to our expectations, no single species gained numerical dominance on vertically oriented sites, which we suggest may result from a diverse species pool at the landscape scale. The relationship between local spider species richness and landscape context has been shown to be pivotal for the increase in spider diversity and abundance (Rusch et al. 2016; Prieto-Benítez and Méndez 2011; Barriga et al. 2010).

The gradient from dry to moist habitats was narrow across vineyard types. However, terraced vineyards had the driest conditions due to their steep embankments and favoured high abundances of xerophilic

species such as *T. quadriguttata*. This confirms the ecological potential of terraced vineyards and supports findings of Košulič et al. (2014), who stressed the role of terrace embankments as refuge and substitute habitats and their great conservation potential for xerothermophilic arthropods.

The diet specialist group was dominated by the ant-eating species *Z. italicum* and showed a collinear increase in abundance with ants in managed vineyards. Gonçalves et al. (2017) also found a positive correlation between ant-eating spiders and ants in vineyards irrespective of management regimes. Ant abundance may be impacted by more open soil surface and higher soil temperatures, both of which are important for ant nesting (Caprio et al. 2015). Consistently, embankments were driest and both ants and *Z. italicum* had the highest abundance in terraced vineyards. The higher abundance of space web weavers in managed vineyards is mainly related to *T. quadriguttata*, which occurred in high abundances on terraced vineyards, likely due to the species' preference for warm and sunny slopes (Gloor et al. 2010). Sheet web weavers were most abundant in vertically oriented vineyards and were dominated by the very common species *A. rurestris*. The dominance of relatively disturbance-tolerant sheet web weavers is in accordance with the high disturbance levels in vertically oriented vineyards.

Similarly to previous studies, we found that changes in vegetation and habitat structure between vineyard types determined spider community composition (Rosas-Ramos et al. 2020; Lafage et al. 2019; Cardoso et al. 2011; Hurd and Fagan 1992). However, compared to earlier work (Schmidt et al. 2007), spider communities showed little response to landscape parameters. The overall high landscape complexity of the study area is likely to decrease the effect (Tscharntke et al. 2005) because almost every site encompassed SNH elements, even within a radius of 150 m. Spider and ground hunter abundance decreased with an increasing cover of SNHs in the surrounding landscape. Initially, this contrasts with findings of other studies that emphasised the importance of SNHs to increase spider abundance (Rusch et al. 2016; Prieto-Benítez and Méndez 2011; Barriga et al. 2010). However, in the study area, SNHs, which mostly consist of vineyard fallows, are already dominant. Hence, our findings do not belittle the importance of SNHs as structural landscape elements but rather reflect the threat of shrub encroachment for ground hunter abundance in consequence of progressive vineyard abandonment. In addition to SNHs, forests add another structural element to the landscape and can be an important source of spider abundance and diversity in vineyards (Hogg and Daane 2010).

For spiders, microhabitat selection on the soil surface is based on a suitable microclimate, reduced predation risk and the availability of prey (Bell et al. 2001; Wise 1993). A high amount of coarse soil particles on slate soils creates harsher conditions with increased temperatures and fewer hibernation sites due to sparser vegetation cover and might, therefore, decrease spider and ground hunter species richness (Taucare-Rios et al. 2018). In contrast, an increasing vegetation cover positively affected the

abundance of spiders and ground hunters as it offers distinct structures and shelter from predators and provides favourable conditions for prey (Podgaiski et al. 2013). Vegetation cover did not exceed 50 %, thus still allowing ground hunter species to move unhindered.

6.5.3 Significance of winegrowing and landscape heterogeneity for spider diversity

Landscape heterogeneity is a key element to maintain and promote biodiversity in agricultural landscapes (Benton et al. 2003). A diverse mosaic of SNHs, forests and vineyards created structural diversity and provided various habitats, thus contributing to an overall high spider diversity in the UMRV.

Managed vineyards, particularly terraced vineyards, supported ant-eating specialists and many xerophilic species adapted to open conditions, whereas vineyard fallows supported highly distinct spider communities including some late-successional species. However, given the progressive abandonment of cultivating vines on steep slopes, we want to emphasise the conservation significance of viticultural management for the maintenance of spider diversity. Contrasting the species pool of managed vineyards and fallows, it becomes evident that nearly 25 % of the species solely occurred on managed sites. Consequently, these species would most likely disappear if vineyards were abandoned. Apart from conservation aspects, traditional management has shaped the cultural landscape for centuries and is of high cultural value for the local population through agronomic as well as touristic activities (Lourenço-Gomes et al. 2015). Therefore, it is fundamental to maintain management activities in steep slope viticulture as the integrity of the cultural heritage and biodiversity depends on winegrowing. We propose vineyard terracing as a valuable approach to keep wine growing on steep slopes financially viable and concurrently provide habitat for spider assemblages that are distinct from both fallows and vertically oriented vineyards.

7. Revegetation of vineyard terrace embankments: A matter of seed mixture and seeding technique



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VW: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing –original draft, Writing – review & editing. **MHE:** Supervision, Writing – review & editing. **IL:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

7.1 Abstract

Maintaining traditional agricultural management to preserve agrobiodiversity remains one of the major challenges for biodiversity conservation in Europe. In Germany, viticulture on steep slopes has shaped cultural landscapes of high conservational value but has declined strongly in recent decades due to insufficient profitability. One promising approach to keep management economically viable is modern vineyard terracing. Here, vineyard rows run parallel to the hillside, thus facilitating management and lowering production costs. At the same time, terrace embankments offer large non-cropped areas between the vines that could make a significant contribution to biodiversity. However, to fully exploit that potential sustainable revegetation of terrace embankments is mandatory but barely studied. For three consecutive years, we evaluated the effects of different seed mixtures (hay threshing, regional and commercial mixture), seeding techniques (manual vs. hydro-seeding), and the effect of nurse plants, hay mulch, and fertilizer on the establishment and maintenance of vegetation on three terraced vineyards in the Upper Middle Rhine Valley, Germany. The regional mixture best met the demands of biodiversity conservation by providing high herb and flower cover. Hay threshing and the regional mixture provided sufficient vegetation cover to reduce the risk of erosion, whereas the commercial mixture performed poorly in terms of vegetation cover and plant diversity. For hydro-seeding, target species richness was higher and bare ground cover was significantly reduced compared to manual seeding. Nurse plants, hay mulch, and fertilizer application only marginally improved plant establishment. Together these results emphasize that hydro-seeding with regional seeds is the best approach for revegetation of vineyard terrace embankments by combining high biodiversity and sufficient vegetation cover to reduce erosion risks at the best cost-benefit ratio for winegrowers. Vineyard terracing contributes to maintaining economically viable viticulture on steep slopes and may concurrently act as a conservation tool for biodiversity in vineyard landscapes.

7.2 Introduction

Maintaining biodiversity in agricultural landscapes remains one of the major challenges for biodiversity conservation in Europe (Pe'er et al. 2017; Kleijn et al. 2011). Traditional small-scale farming contributed to the creation of entire landscapes, cultural traditions, and biodiversity (Batáry et al. 2015; Paiola et al. 2020). These systems often maintain high biodiversity and are best preserved by continuing extensive management practices (Henle et al. 2008; Sutcliffe et al. 2015). However, current trends are to either intensify or abandon land use, both of which are threatening biodiversity (Loos and Wehrden 2018).

Viticulture on steep slopes has shaped cultural life and landscapes of high aesthetic and conservational value of entire regions (Lourenço-Gomes et al. 2015). In Germany, much of the traditional small-scale cultivation on dry-stone walls faced intense transformation over the last century. To enhance productivity, vineyards were planted in a downhill direction on steep slopes, thus increasing mechanization as well as the area under cultivation. However, in recent years steep slope vineyards have increasingly been abandoned due to insufficient profitability. The progressive expansion of fallow land (up to 39% in the Middle-Rhine Valley; 1987 – 2019)(Stoll and Schultz 2020) threatens the preservation of the cultural heritage as well as the flora and fauna associated with vineyards.

One promising approach to keep management economically viable and hence halt the decline of viticulture on steep slopes is modern vineyard terracing (Strub and Loose 2021a). In this approach, vineyard rows run parallel to the hillside, thus facilitating trafficability, lowering production costs, and improving occupational safety. At the same time, a substantial area (more than 50%) is composed of embankments that are left uncultivated and managed extensively (no fertilizer and pesticide application, no tractor driving). Slope inclination of embankments depends on several factors such as soil depth, parent rock, soil type, and inter-row width and usually ranges from 45 – 48° (Wehinger and Spies 2008). From a conservationist's perspective, embankments offer enormous potential to establish species-rich plant communities within the agricultural system, that could act as biodiversity refugia (Wersebeckmann et al. 2021; Košulič et al. 2014) and might even play a role in habitat networking. However, active introduction of target species appears necessary, since the local diaspore bank is usually poor in grassland species and nearby seed sources are missing (Török et al. 2011). From a practitioner's point of view, a permanent vegetation cover on embankments is foremost needed to prevent soil loss and maintain stability (Pijl et al. 2020; Rodrigo-Comino et al. 2019; Novara et al. 2011). Indeed, spontaneous colonization has turned out to be insufficient, and unpredictable and has yielded unsatisfactory results about rapid vegetation cover under harsh arid conditions on embankments (Bochet et al. 2010a). To overcome these constraints, active revegetation seems mandatory to establish species-rich vegetation that tackles both erosion prevention and nature conservation purposes.

7. Revegetation of vineyard terrace embankments: A matter of seed mixture and seeding technique

Considering the environmental conditions of steep and usually south exposed terrace embankments, especially against the background of climate change, conditions for seedling recruitment and initial plant establishment are extremely challenging. To protect vulnerable seedlings against drought and solar radiation application of a mulch layer can improve soil moisture capture and retention (Auestad et al. 2016; Baasch et al. 2012). Nurse plants have similar effects as they rapidly grow and thus create 'safe sites' for seedling recruitment but gradually vanish as more competitive or better-adapted species colonize (Durbecq et al. 2022; Elmarsdottir et al. 2003). An initial fertilizer application can further help to improve soil properties and thus enhance plant establishment, particularly on slopes with sparse humus layers (Tormo et al. 2007). To date, no studies on such methods to assist plant establishment on vineyard terrace embankments in Central Europe (Germany), exist.

Based on the practitioner's experience, not only seedling recruitment but also maintenance in the long term turned out to be critical. Consequently, the selection of species able to thrive under those conditions, including local soil conditions, is essential for revegetation success (Bochet et al. 2010b). Nevertheless, knowledge about well-performing, sustaining seed mixtures and application techniques (e.g. hydro-seeding) for vineyard terrace embankments, is missing.

Finding a viable and affordable strategy to revegetate vineyard terrace embankments that addresses the needs of biodiversity, erosion mitigation, and takes up the challenges of climate change at the same time, is demanding. Therefore, this study aims to address key issues in the revegetation of modern vineyard terrace embankments:

1. Which seed mixtures for vineyard terrace embankments
 - a. promote and maintain a flower- and species-rich vegetation to benefit biodiversity
 - b. provide a sufficient vegetation cover to reduce the risk of erosion and stabilize embankments
 - c. and hold a good cost-benefit ratio for practitioners?
2. Do seeding techniques and the use of nurse plants have a significant effect on vegetation cover, thereby reducing the risk of erosion?
3. Do hay mulch and initial fertilizer enhance plant establishment?
4. Do local soil conditions affect species richness and community composition?

The main contribution of our study is to develop a revegetation strategy for terrace embankments since they present a major opportunity for a sustainable form of steep slope viticulture that contributes to the preservation of cultural landscapes, biodiversity conservation and secures the livelihood of the local winegrowers.

7.3 Material and Methods

7.3.1 Study area and design

The study was situated in the wine-growing region of the Upper Middle Rhine Valley (UMRV), Germany. Three terraced vineyards were constructed in March 2018 on the site of former vertically oriented or fallow vineyards (Vineyard A: Assmannshausen 49.9942°N, 7.877058°E, Vineyard B: Lorch 50.038597°N, 7.817103°E, Vineyard C: Rheindiebach: 50.040489°N, 7.7869°E). All study sites had silty loam and slightly chalky soils of moderately alkaline pH (7.2 – 7.5). The annual temperature averages 11.64 °C and the annual precipitation is 554.14 mm (Lorch, 2015-2019, weather station Hochschule Geisenheim).

In early April 2018, we established a replicated design to study the effects of three different seed mixtures, two different seeding techniques, and the effect of nurse plants, hay mulch, and fertilizer on the establishment, composition, and maintenance of perennial vegetation on vineyard terrace embankments (Figure 26). We tested hydro-seeding of (1) a commercial cultivar mixture (RSM 7.22), (2) a regionally adapted wildflower mixture, and (3) a hay threshing, that was harvested in July 2017 from two local species-rich meadows at a maximum distance of 10 km from the study sites. The commercial mixture represents the best available biodiverse standard mixture (DIN 18917; 23 species, 3.1% herbs, 96.9 % grasses) that is explicitly recommended for reclamation of dry sites and extensively used areas (see Table E. 1, supplementary material for the complete species list). The regional wildflower mixture was compiled in collaboration with a regional seed producer (39 species, 30% herbs, 70% grasses) (Table E. 1). All species were of regional provenance, adapted to the local abiotic conditions, and chosen to benefit multiple insect species (Carrié et al. 2012). We followed manufacturer specifications on sowing application rates: 20 g/m² of seeds for commercial mixture, 5 g/m² for regional mixture, and 25 g/m² of seeds for hay threshing. The hydro-seeding suspension contained water, organic glue (25 g/m² guar flour), cellulose mulch (80 g/m²), and the respective seed mixture.

To isolate the effects of seeding techniques from that of seed mixtures, the regional mixture was applied manually and via hydro-seeding. Before manual application, embankments were roughened to facilitate seed attachment. To avoid segregation of seed sizes and to facilitate the manual application we added bruised maize to the seed mixture (15 g/m²). Further, each of the three seed mixtures and the two seeding techniques were sown in a treatment with and without additional nurse plants (3 g/m² of *Bromus secalinus*, *Papaver rhoeas*, *Centaurea cyanus*). On five embankments per vineyard site, the resulting eight treatments were randomly assigned with one replicate per embankment at a length of 10 m each (Figure 26 A). Embankment's width ranged from 1.30 – 2.70 m among sites but was more similar within sites.

7. Revegetation of vineyard terrace embankments: A matter of seed mixture and seeding technique

We set up an additional study to evaluate the effects of hay mulch, fertilizer, and nurse species on initial vegetation development and used the hydro-seeded regional mixture as a foundation (Figure 26 B). Treatments with an additional mulch layer were covered with 400 g/m² hay (*Festuca rubra* agg.; second cut, seed-poor hay). Additional fertilizer (50 g/m² of mineral NPK - fertilizer (18(N)-7(P)-10(K))) was applied manually after hydroseeding. Control plots did not receive any additional treatment. Every treatment was also sown with and without additional nurse plants.

To gain an overview of species emerging from the diaspore bank, three plots (length of 6 m each) remained unseeded and were established randomly across each vineyard. To ensure stability and prevent erosion, all embankments that were not part of the study were hydro-seeded with the regional mixture. In the first year after implementation, all plots were mown manually in August. In all subsequent years, mulching was done in July.

7. Revegetation of vineyard terrace embankments: A matter of seed mixture and seeding technique

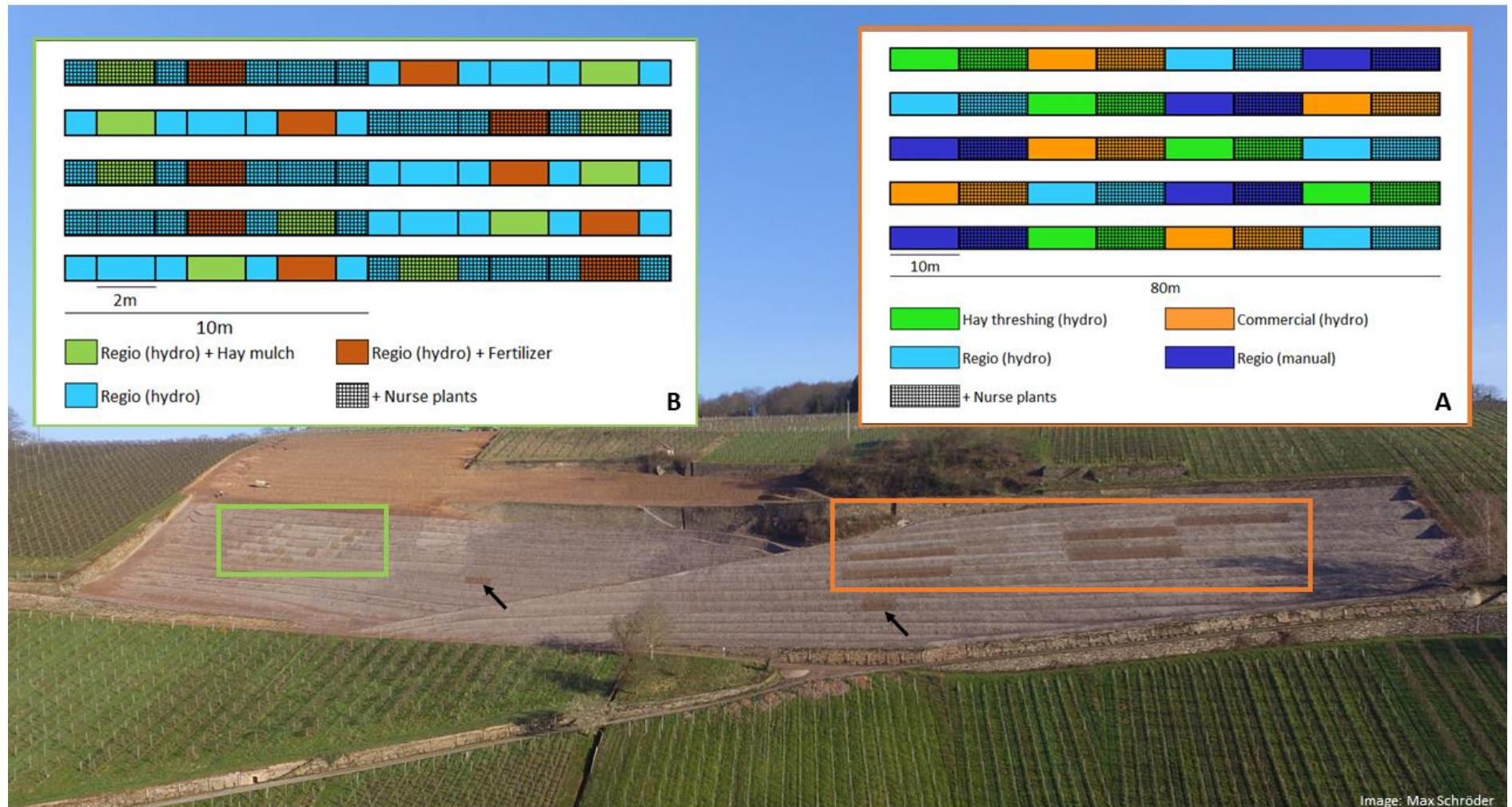


Figure 26: One of three revegetated vineyards with three different seed mixtures (hay threshing, commercial mixture, regional mixture) and two seeding techniques (manual and hydro-seeding) (orange box, A) and different additives to support plant establishment (hay mulch, fertilizer, nurse plants (+/-)) (green box, B) that were applied in a replicated design in 2018. Within the orange box, bright areas represent hydro-seeded and dark areas show manually seeded plots. Black arrows show two of three unseeded plots.

7.3.2 Vegetation-related measures

Vegetation establishment and composition were assessed in three consecutive years (2018 – 2020) for all treatments (seed mixtures, seeding technique, hay mulch, fertilizer, nurse plants). Vegetation surveys were carried out once a year (June - July) using permanent plots of 6m² for study A, and 2m² for study B (replicates per treatment at each site: n = 5). In the unseeded plots, species emerging from the diaspore bank were also assessed annually in permanent plots of 6m² (replicates per site: n = 3). Within each plot, the cover of all vascular plant species was visually estimated using a Londo scale (Londo 1976), and the percentage of vegetation, bare ground, and litter cover were assessed. Taking the vegetation cover as 100 %, the percentage of herb and grass cover was visually estimated. All cultivars of *F. rubra* were summarised as *F. rubra* since they could not be distinguished. The coloured flower cover of all currently flowering plants was visually estimated for all species together on each sampling event in five classes (<1 % = very low; 5–15 % = low; 15–50 % = medium; 50-75 % = high; >75 % = very high) and used as a proxy for the conservational value e.g., by benefiting flower-visiting insects. Vegetation height was measured in 2019 and 2020 using a yardstick (five random measurements per plot).

7.3.3 Soil parameters

Soil samples of each treatment were taken to a depth of 10 cm (mixing of 8 soil core samples per treatment) in 2018 and 2020. All samples were dried at 40 °C and sieved to retain particles above 2 mm. All measurements were conducted according to the standard guidelines issued by the association of German agricultural analytic and research institutes (Verband deutscher landwirtschaftlicher Untersuchungs- und Forschungsanstalten e.V. 1991). Samples were analysed for soil type, pH, plant-available phosphorus (P), potassium (K), magnesium (Mg), and carbon-to-nitrogen ratio (C:N). Soil type was determined using a texture triangle. The sand proportion was isolated by wet sieving and silt and clay were separated via sediment analysis. For pH measurements, samples were mixed with a 0.01 M calcium-chloride solution and measured three hours after application. To determine plant-available P and K, the soil samples were blended with calcium-acetate-lactate extract. For photometer measurements, P was stained with ammonium-molybdate, while K content was determined via a flame photometer. For the measurement of Mg, soil was mixed with a calcium chloride solution, and its suspension was measured in an atomic absorption spectrometer. For the determination of C and N, an elemental analyser using combustion and following gas chromatography in the thermal conductivity detector was used. The C:N ratio was calculated, and organic matter content was assessed by multiplying the C content by the factor of 1.724. All methods are described in Schaller (2000).

7.3.4 Data analysis

All statistical analyses were carried out using the R environment (R Core Team 2020). Figures were created with ggplot2 (Wickham 2016), cowplot (Wilke 2019), and Excel (2019).

To evaluate the effects of the different treatments studies A (seeding technique, seed mixtures) and B (nurse plants, fertilizer, mulch) were analysed separately. For an analysis of the seeding technique (manual vs. hydroseeding), only the regional mixture from study A was considered and for evaluation of the three seed mixtures, we only compared hydro-seeded treatments of study A.

Some of the sown species also appeared in the unseeded control plots. Therefore, we could not differentiate whether seedlings of our plots emerged from the mixture or the diaspore bank. Seedlings of main shared species in unseeded plots in 2018 such as *Achillea millefolium* (1 – 3 % cover), *Daucus carota* (1 – 5 % cover), and *Medicago lupulina* (1 – 3 % cover) are likely to be remnants of past inter-row vegetation from former vineyards. Hence, we down-weighted their abundance by subtracting the species mean abundance of the control plot from the respective species abundance in each surveyed plot (site-specific). Vegetation cover of unseeded plots was different between vineyards, but due to the limited width of 6 m, the unseeded plots were not considered for further statistical analysis (Table E. 3).

7.3.4.1 Multivariate analysis

To analyse differences in plant species composition in relation to seed mixture and seeding technique, a preliminary detrended correspondence analysis (DCA) was performed (package: vegan) (Oksanen et al. 2020). We considered the length of the gradient of the DCA as a measure of the species turnover (Lepš and Šmilauer 2010). For a length of gradient < 3 (1st axis) we chose a linear model and conducted a Principal Component Analysis (PCA) (package: vegan). Vegetation and soil parameters that were significantly related to the PCA axes ($p < 0.05$, based on a permutation test with 9999 permutations) were included post-hoc by projection. To reduce the influence of dominant species, we $\log_{10}(x + 1)$ transformed the community data and excluded species with less than three occurrences from the analysis. All vegetation and soil variables were standardized to zero mean and unit variance before the analysis (function “scale”, package: vegan). Principal component analysis showed a clustering of plant communities among vineyard sites on the first principal component (Figure 28). To determine, whether differences were masked by vineyard sites we subtracted sites by subsequently performing a Partial PCA on the remaining residual variance.

7.3.4.2 Univariate Analysis

We chose (generalized) linear mixed effect models (GLMMs) with following post-hoc tests to analyze differences between seed mixtures, seeding techniques, hay mulch, fertilizer, and nurse plants on species richness and cover of vegetation, bare ground, litter, herbs, and grasses (function “glmmTMB”,

package: glmmTMB; (Brooks et al. 2017). For ordinal data (flowers) we used ordered regression models (function “clmm”, package: ordinal (Christensen, 2019)). Post-hoc-tests were applied using the emmeans package (Lenth, 2020). To account for the hierarchical nesting of the study design, ‘Vineyard/Embankment/Paired plot’ (paired plot = nurse/no nurse plants) was added as a random effect to each model. Data exploration was conducted according to the protocol of Zuur et al. (2010). For continuous data, Gaussian distribution was used. For count data, we used Poisson distribution. If overdispersion was detected we used negative binomial and in case of underdispersion, Conway-Maxwell-distribution. If pair-wise comparisons between treatments with and without additional nurse plants revealed no significant differences, data for respective seed mixtures and seeding techniques were pooled for further analysis. For correlations between soil parameters, plant species richness, and target species richness we used Pearson correlation coefficients (function “chart.correlation”, package: PerformanceAnalytics (Peterson and Carl 2020)). Target species comprised all species that were introduced by sowing. For hay threshing target species richness could not be calculated since species composition was unknown.

7.4 Results

7.4.1 Seed mixtures

Vegetation, bare ground, and herb cover did not differ significantly between seed mixtures in 2018 (Figure 27 A-C). From 2019 onwards, the regional mixture had significantly higher vegetation (Figure 27 A) and significantly lower bare ground cover than the commercial mixture (Figure 27 B). Herb cover was significantly highest for the regional mixture and lowest for the commercial mixture (Figure 27 C). Vegetation height was significantly higher for the regional mixture compared to the commercial mixture and the hay threshing in 2020, while there was no difference in 2019 (Figure 27 D).

7. Revegetation of vineyard terrace embankments: A matter of seed mixture and seeding technique

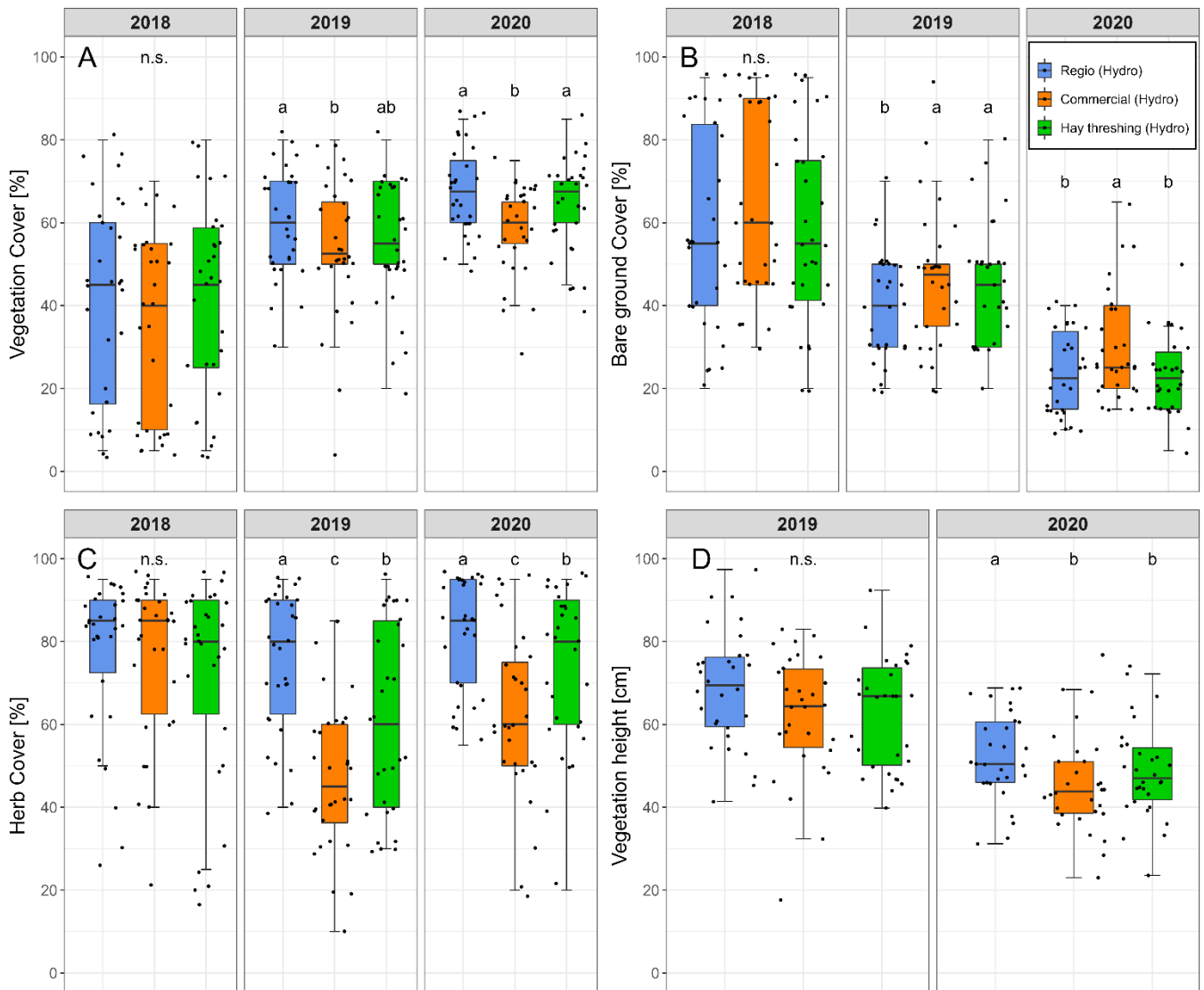


Figure 27: Boxplots show differences between hydro-seeded mixtures from study A (2018 – 2020) for vegetation (A), bare ground (B) and herb cover (C), and vegetation height (D) analysed using LMMs. Each data point represents a surveyed plot. Different letters indicate significant differences. Non-significant differences are indicated by n.s.

Analysis of soil parameters in 2020, showed a significant positive correlation between species richness of all mixtures and pH value (Table 13, Figure E. 1). For target species richness of the regional and the commercial mixture, the effect was even more pronounced (Table 13, Figure E. 1). On the contrary, there was a significant negative correlation between potassium, phosphorous, and magnesium levels and species richness (Table 13, Figure E. 1) and target species richness of the regional mixture (Table 13, Figure E. 1). Species richness of the commercial mixture and phosphorus and magnesium were negatively correlated (Table 13, Figure E. 1, while target species richness of the commercial mixture and potassium and phosphorous showed a negative correlation (Table 13, Figure E. 1). There was no correlation between species richness of the hay threshing and any of the soil parameters, except for pH (Table 13, Figure E. 1).

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Table 13: Correlation between species richness of regional mixture, commercial mixture, hay threshing, target species richness of regional mixture and commercial mixture, and soil parameters pH, K, P, and Mg for 2020. Pearson correlation coefficients are given. Asterisks indicate significance levels ($p < 0.05=*$, $p < 0.005=**$, $p < 0.001=***$).

	pH	K	P	Mg
Species richness				
Commercial	0.46*	-0.019	-0.52**	-0.37*
Hay threshing	0.56**	-0.003	-0.0023	-0.066
Regio (Hydro)	0.79**	-0.47**	-0.50**	-0.55**
Target species richness				
Commercial	0.68***	-0.42*	-0.33*	-0.20
Regio (Hydro)	0.74***	-0.61***	-0.025	-0.33*

Plant communities of seed mixtures showed a distinct clustering between vineyard sites throughout the years (Figure 28 B, E, H). Soil and vegetation-related parameters were correlated to the PCA-Axes, while for the Partial PCA, where the focus was on treatment effects within vineyards, only vegetation-related parameters such as herb, vegetation, and flower cover remained correlated to the PCA-Axes. From 2019 onwards, plant communities were clustered regarding seed mixtures even though clustering of vineyard sites was still visible. Partial PCA results of 2019 revealed distinct clustering of the commercial mixture and the regional mixture with the hay threshing in between (Figure 28 F). In accordance with the results shown in Figure 27, the regional mixture was associated with increased vegetation height as well as a higher herb and flower cover, while the commercial mixture was positively correlated with high grass cover (Figure 28 F). In 2020, plant community composition was almost completely different between the regional and the commercial mixture (Figure 28 G), which was even more pronounced in the partial PCA (Figure 28 I). Here, plant communities of the regional mixture were positively correlated with higher herb, vegetation, and flower cover while the commercial mixture was again associated with higher grass cover (Figure 28 I).

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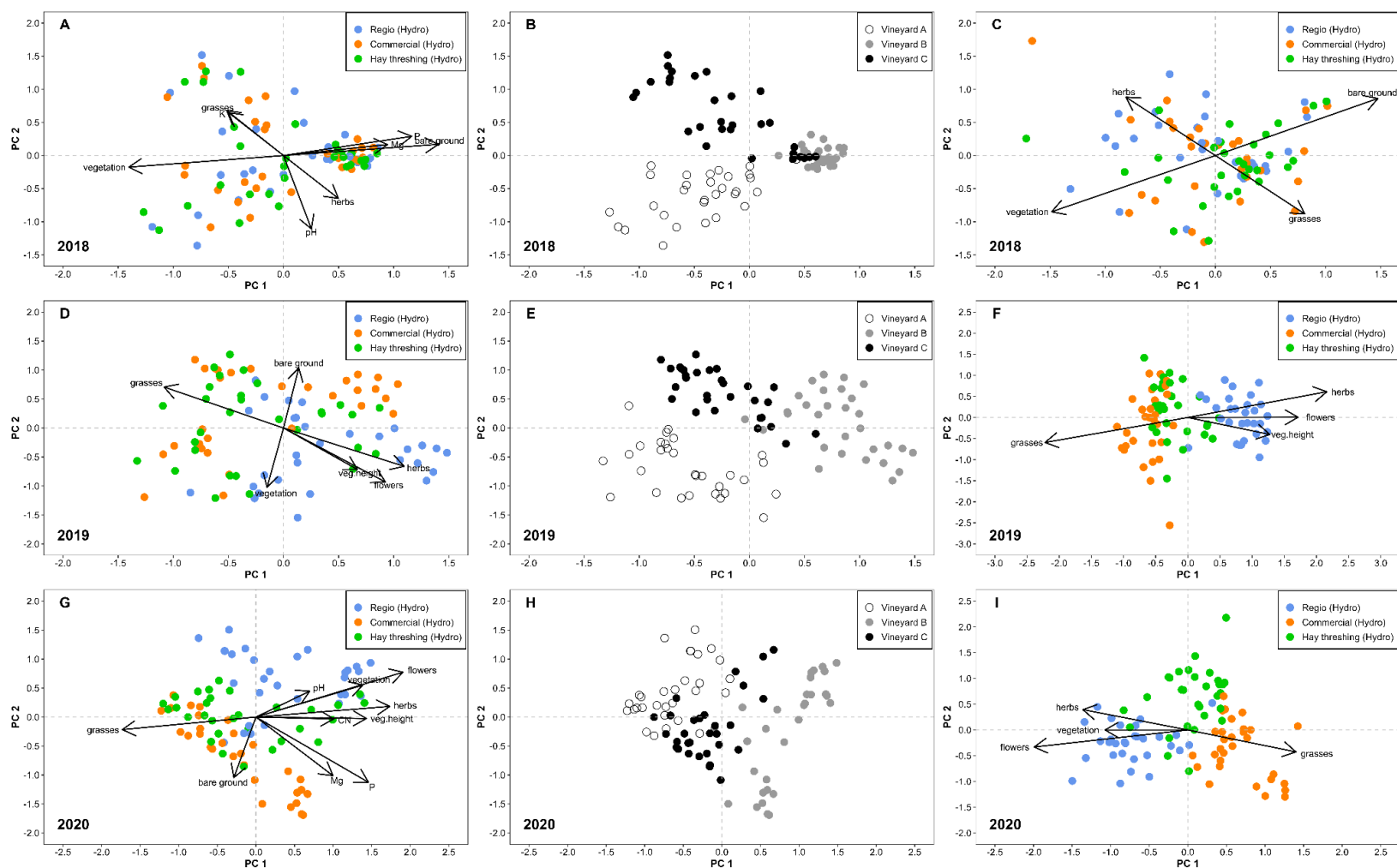


Figure 28: PCA and partial PCA results for plant species composition of seed mixtures for 2018 - 2020. Graphs show PCA scores for seed mixtures (A, D, G) and sites (B, E, H) and partial PCA scores for seed mixtures after accounting for site differences (C, F, I). Sample scores for regional seed mixtures are displayed in blue, scores for commercial seed mixtures are displayed in orange, and scores for hay threshing are displayed in green. Site scores are displayed as white (Vineyard A), grey (Vineyard B), and black (Vineyard C) dots. Environmental parameters that were significantly related to the PCA axes ($p < 0.05$, 9999 permutations) were included post-hoc by projection.

7.4.2 Seeding technique

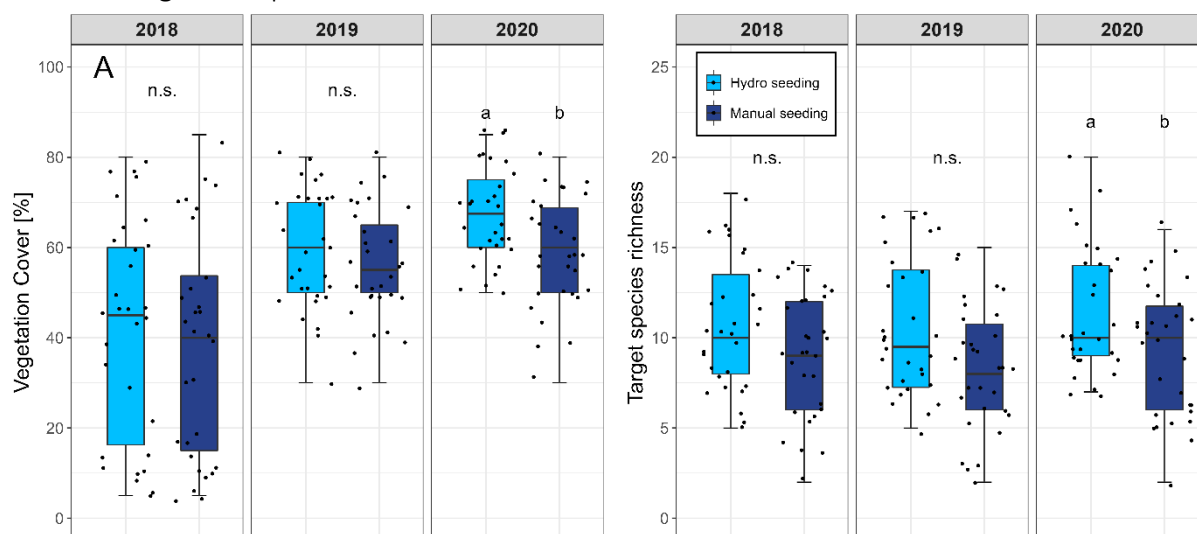


Figure 29: Boxplots show differences between vegetation cover (A) and target species richness (B) of two different seeding techniques (N=30) for the regional mixture of study A (2018-2020) analysed using (G)LMMs. Each data point represents a surveyed plot. Different letters indicate significant differences. Non-significant differences are indicated by n.s.

Manual seeding had a significantly lower vegetation cover in 2020 (Figure 29 A) and a significantly lower target species richness from 2019 onwards (Figure 29 B). Herb and grass cover differed significantly only in 2018 with the hydro-seeding having a higher herb and a lower grass cover (Table E. 2). Vegetation height was higher for the hydro-seeding in 2019 but significantly higher for the manual seeding in 2020 (Table E. 2). Plant communities were not significantly different between seeding techniques (Figure E. 4).

7.4.3 Hay mulch, Fertilizer, Nurse Plants

Hay mulch led to a 60-fold higher litter cover and reduced bare ground cover by approx. 40 % in the first year compared to the treatments without mulch (Table 14). In addition, grass cover was almost doubled in the hay mulch treatment in the first year, but only in the presence of nurse plants. None of these differences persisted into the 2nd or 3rd year, except for a slightly higher litter cover of the mulch treatment with nurse plants (Table 14). Also, the fertilized treatment with no nurse plants developed slightly higher litter cover in year 3. Vegetation cover was significantly lower for the mulch layer without nurse plants compared to the fertilizer treatment with nurse plants in the first year (Table 14). Vegetation height differed between treatments only in year 2, where it was highest in the mulch treatment without nurse plants, and lowest in the fertilized and control treatment without nurse plants. Target species richness did not differ significantly between treatments.

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Table 14: Effects of fertilizer, hay mulch, and nurse plants (N+/N-) on local vegetation parameters and target species richness (N = 15). The percentage proportion of herb and grass cover was estimated within the total vegetation cover. (G)LMMs were used with 'site/embankment/paired plot' as a random factor. Different letters indicate significant differences between treatments ($p < 0.05$).

	Year	Control N-	Control N+	Fertilizer N-	Fertilizer N+	Hay mulch N-	Hay mulch N+
Vegetation cover [%]	2018	43.67 ^{ab} ± 5.06	45.00 ^{ab} ± 5.16	42.00 ^{ab} ± 4.39	49.67 ^a ± 4.32	31.67 ^b ± 3.98	41.33 ^{ab} ± 3.43
	2019	46.67 ± 4.52	51.33 ± 4.40	46.33 ± 4.27	53.67 ± 4.35	51.67 ± 4.36	48.67 ± 4.79
	2020	62.00 ± 3.51	60.00 ± 3.87	59.67 ± 3.53	59.33 ± 3.71	63.00 ± 4.12	62.00 ± 3.48
Bare ground cover [%]	2018	56.67 ^a ± 5.06	55.00 ^a ± 5.16	57.67 ^a ± 4.47	50.00 ^a ± 4.50	9.33 ^b ± 2.43	4.67 ^b ± 1.03
	2019	47.67 ± 3.65	46.00 ± 4.00	51.00 ± 3.91	43.33 ± 3.33	43.33 ± 4.16	40.67 ± 3.78
	2020	28.33 ± 3.71	29.67 ± 3.02	28.50 ± 3.22	30.83 ± 3.02	27.67 ± 3.99	26.00 ± 3.01
Litter cover [%]	2018	0.33 ^b ± 0.33	0.00 ^b ± 0.00	0.33 ^b ± 0.33	0.33 ^b ± 0.33	64.00 ^a ± 3.72	57.33 ^a ± 3.58
	2019	5.67 ^b ± 2.71	2.67 ^b ± 1.18	2.67 ^b ± 4.95	3.00 ^b ± 1.53	5.00 ^b ± 1.19	10.67 ^a ± 2.28
	2020	8.00 ^b ± 0.89	7.83 ^b ± 1.26	10.50 ^a ± 1.43	8.83 ^b ± 1.90	8.00 ^b ± 1.15	10.0 ^a ± 1.62
Grass cover [%]	2018	15.67 ^a ± 3.55	15.33 ^a ± 2.60	16.67 ^a ± 4.99	17.00 ^a ± 4.39	17.33 ^a ± 3.19	31.67 ^b ± 6.67
	2019	23.00 ± 6.10	24.33 ± 5.32	21.33 ± 6.54	23.33 ± 6.07	24.00 ± 6.25	19.67 ± 5.01
	2020	17.33 ± 3.55	13.00 ± 2.38	19.00 ± 4.02	19.00 ± 4.09	21.00 ± 3.91	14.33 ± 2.96
Herb cover [%]	2018	84.33 ± 3.55	84.67 ± 2.60	83.33 ± 4.99	83.00 ± 4.39	82.67 ± 3.19	68.33 ± 6.67
	2019	77.00 ± 6.10	75.67 ± 5.32	78.67 ± 6.54	76.67 ± 6.07	76.00 ± 6.25	80.33 ± 5.01
	2020	82.67 ± 3.55	87.00 ± 2.38	81.67 ± 4.02	81.00 ± 4.09	79.00 ± 3.91	85.67 ± 2.96
Vegetation height [cm]	2018	-	-	-	-	-	-
	2019	55.79 ^b ± 3.74	59.12 ^{ab} ± 3.81	58.01 ^b ± 3.46	63.20 ^{ab} ± 4.44	74.49 ^a ± 4.98	64.00 ^{ab} ± 4.20
	2020	49.04 ± 3.16	51.60 ± 2.52	53.97 ± 3.85	49.35 ± 3.10	50.40 ± 3.53	50.95 ± 3.52
Target species richness	2018	5.87 ± 1.04	5.53 ± 1.01	5.53 ± 1.04	5.73 ± 1.12	6.20 ± 0.96	6.13 ± 1.04
	2019	5.93 ± 0.98	6.13 ± 1.01	5.33 ± 1.10	5.33 ± 1.11	5.67 ± 0.98	6.80 ± 0.96
	2020	6.20 ± 1.04	6.00 ± 1.06	6.10 ± 0.97	6.40 ± 0.91	5.87 ± 0.90	6.27 ± 1.28

7.5 Discussion

7.5.1 Seed mixtures

Our results substantially improve the understanding of proper revegetation of vineyard terrace embankments that meets the demands of biodiversity conservation and provides a sufficient vegetation cover to reduce the risk of erosion at a reasonable cost-benefit ratio for practitioners. Together, our results confirm that regional seeds were most effective in establishing high vegetation, herbaceous, and flower cover (Figure E. 2). Hay threshing had moderate performance in terms of herbaceous and flower cover (Figure E. 2), whereas the commercial mixture performed poorly regarding vegetation cover. However, all mixtures successfully germinated despite the drought conditions in 2018 (Figure E. 3). Together with species emerging from the diaspore bank the regional mixture and the hay threshing immediately provided a vegetation cover of more than 40 % which, according to Andrés and Jorba (2000) is needed to prevent severe erosion on embankments.

Even though, mixture-related differences became evident in community composition, in the year of implementation, the effect of vineyard sites prevailed. Site-specific differences were mainly based on different soil characteristics and species emerging from the diaspore bank. In 2018, common field weeds (e.g. *Elymus repens*, *Chenopodium album*), dominated the community and contributed to the vegetation cover while perennial species from the mixtures mainly developed vegetative plant parts (basal leaves, rosettes) as reproductive plant parts developed later. In subsequent years, this relation reversed, and mixture-related differences increasingly determined community differentiation although the influence of vineyard-specific properties (e.g. pH) was still visible.

Even though herb cover was significantly lowest for the commercial mixture, a direct comparison of herbaceous cover and plant diversity of mixtures remains not entirely accurate since the proportion of herbaceous species was different among the seeding sources. Remarkably, bare ground cover was significantly higher for the commercial mixture although the seeding application rate was four times as high as for the regional mixture. This indicates a higher failure rate of commercial seeds compared to the regional mixture. Poor ecological performance and higher failure rates of non-regional mixtures have been reported also by other authors (Auestad et al. 2016; Zelnik et al. 2010) as these mixtures are composed of various seed sources without taking local site conditions into account (Conrad and Tischew 2011).

Threshing of seeds from species-rich grasslands is a well-established method to restore target communities but the seed content is hard to control and dependent on factors such as time and frequency of harvesting (Kiehl et al. 2010). Seeds of species flowering early in the year might already be shed and lost before the hay is collected resulting in incomplete species communities (Scotton 2016). To gather a wide range of species that include early and late fruiting species, repeated harvesting

throughout the season is recommended (Bischoff et al. 2018; Edwards et al. 2007). Based on our results, the moderate performance of hay threshing regarding herbaceous and flower cover could be partly explained by an insufficient number of seeds. The low number of species found in the hay threshing plots could be the consequence of inefficient threshing and insufficient time and frequency of harvesting since the hay threshing itself has been successfully used for transferring species-rich grasslands (Schaumberger et al. 2021; Edwards et al. 2007). To obtain a higher proportion of herbaceous species, harvesting dates should be extended and also combined with hand collecting which in turn would greatly increase effort and costs (Kiehl et al. 2010). Due to the time offset between terrace construction and revegetation early in the year and harvesting time in summer, costs and seed transfer efficiency cannot be reduced by the transfer of freshly cut material (Scotton and Ševčíková 2017; Kiehl et al. 2010). Considering the already high costs for the production of hay-thresh in our study (harvesting and processing: ≈ 31000 €/ha), this approach does not seem an affordable and feasible method for winegrowers. Nevertheless, hay threshing could be reasonable for the revegetation of vineyard terrace embankments, if specific conservation objectives and the restoration of valuable local plant communities are pursued.

At present, it is often argued that costs for regional seeds are substantially higher than for commercial ones, but this difference is largely levelled out by the lower seeding density required for regional seeds, even if the influence of different seed weights cannot be excluded at this point. Regional mixtures with $3 - 5 \text{ g/m}^2$ cost $1500 - 2600$ €/ha, while 20g/m^2 of commercial mixtures amount to 1800 €/ha. Moreover, the better adaptability and performance of regional mixtures ensure maintenance and stability in the long term, thus contributing to sustainable vegetation cover and benefits for biodiversity and erosion mitigation. Locally increased soil pH had a positive influence on species richness as also observed by Barlow et al. (2020) in the context of restoring pipeline corridors. We observed a general trend for a negative correlation between nutrient levels and species and target species richness, particularly for the regional mixture. Such patterns are widespread (La Riva et al. 2011) and emphasize the need for an appropriate management regime to maintain plant species richness. For long-term persistence, regular mowing with subsequent biomass removal, and thereby nutrient impoverishment appears to be mandatory (Tälle et al. 2018; Haaland et al. 2011). Alternate mowing of e.g. every 2nd of the embankments will further increase heterogeneity, ensure the availability of nectar and pollen sources during the whole vegetation season, and act as a refuge and hibernation site (Buri et al. 2014). The optimal mowing date and technique should be the subject of further studies, also considering the nesting periods of regionally endangered birds such as the rock bunting (*Emberiza cia*) that may nest in the embankments (VW, personal observation).

7.5.2 Seeding technique

In the year of implementation, both, hydro- and manual seeding reached a vegetation cover of nearly 40 % which is necessary for slope stabilization and erosion prevention as described for highly erosion-sensitive slopes (Andrés and Jorba 2000). Although vegetation cover was significantly higher for hydro-seeded plots, manual sowing of the regional mixture had a slightly higher vegetation cover than the hydro-seeded commercial mixture. Studies on motorway embankments in Spain, where hydro-seeded commercial mixtures failed due to insufficient adaptation, also concluded that hydro-seeding itself did not guarantee sufficient vegetation cover, but that the seed's nativeness and adaptation to local site conditions are of major importance (García-Palacios et al. 2010; Tormo et al. 2007). However, as manually applied seeds are not stuck to the embankments they are much more exposed to environmental risks and are particularly prone to be washed and blown off in the early development stages (Elmarsdottir et al. 2003). A long period of drought together with a heavy rainfall event that occurred a few weeks after seeding (Fig. E 3, supplementary material) is likely to have washed off seeds from the manually seeded plots, thus resulting in a significantly lower target species richness, lower vegetation cover and vegetation height in subsequent years. Looking ahead, climate change will increase the frequency and severity of extreme weather events such as heavy rainfalls (Fischer and Knutti 2015), and therefore hydroseeding combined with regional seeds appears to be the most promising approach for revegetation of vineyard terrace embankments.

7.5.3 Hay mulch, fertilizer and nurse plants

Our results showed relatively small and short positive effects of hay mulch in significantly reducing bare ground cover in the year of implementation. Grass cover was significantly higher with an additional mulch layer since it promoted the growth of the nurse grass *Bromus secalinus*. However, that effect was especially pronounced in one particular vineyard. The protective mulch layer did not significantly support or facilitate germination of target species by creating more favourable microclimatic conditions as has been described in previous studies (Baasch et al. 2012; Tormo et al. 2007). Nevertheless, a mulch layer can work as effective erosion control on embankments (Kirmer et al. 2012). Results on fertilizer amendments included in hydro-seeding are contrasting. For one thing, on degraded and reclaimed sites with poorly developed soils, fertilizer application enhanced plant establishment (Tormo et al. 2007; Elmarsdottir et al. 2003) but on the other hand, nutrient availability favours fast-growing generalist species over the more conservation-relevant target species (Oliveira et al. 2013; García-Palacios et al. 2010). In our study, fertilizer application marginally enhanced vegetation cover in 2018, but given the very small effect and good resource availability on terraced vineyards, the application of fertilizer on embankments appears superfluous. Furthermore, higher nutrient levels had rather an adverse effect on target species richness. Nurse species are mainly used for erosion control and to facilitate the initial establishment of target species by improving microclimatic conditions at the beginning of revegetation

efforts (Zelnik et al. 2010). In our study, nurse plants did not significantly enhance vegetation cover, their performance was highly variable between species and sites and a major proportion only emerged in 2019 thus missing the target to provide rapid vegetation cover. Extremely hot and dry environmental conditions on vineyard embankments seemed to be detrimental to nurse plant emergence and the low performance of nurse plants on semiarid road slopes has been reported earlier (Bochet et al. 2010b; Albaladejo et al. 2000). This is also evident from the positive response of *B. secalinus* to hay mulch which likely improved soil moisture. However, from our results, the performance of nurse plants was not very conclusive and, given the fact that the regional mixture and hay threshing provided sufficient vegetation cover, nurse plants did not add further benefits for initial plant establishment on terrace embankments.

7.6 Conclusion

Revegetation of vineyard terrace embankments with regional seeds and hydroseeding best meets the demands of biodiversity conservation and practitioners' needs. Regional seeds and hay threshing provided higher vegetation, herb, and flower cover compared to non-regional commercial seeds. High nutrient levels had an adverse impact on plant species richness. Thus, to maintain plant species richness regular mowing with subsequent biomass removal and nutrient impoverishment seems mandatory. Our findings demonstrate a straightforward revegetation strategy that can be easily applied by practitioners and should forward the inclusion of appropriately managed vineyard terrace embankments into agri-environmental schemes. The knowledge gained in this study can be further transferred to the cultivation of other perennial crops on modern terraces, and any revegetation measures of steep and erosion-sensitive embankments such as motorways.

8. Discussion, Synthesis and Perspectives

In summary, the small-structured viticultural landscape of the UMRV supported high species diversity, high numbers of rare and threatened species and diverse species communities across managed and abandoned vineyards. There was no uniform positive effect of one vineyard type on all investigated groups. Instead, the responses were rather group and taxon specific and driven by distinct vineyard management intensities, local vegetation structures, local soil conditions and the surrounding landscape (Figure 30). Heterogeneous landscapes including actively managed and abandoned vineyards as well as natural elements provided multiple resources that were critical to fulfill the species-specific needs of numerous species. However, to preserve the characteristic flora and fauna of steep slope viticultural landscapes, active vineyard management is essential. Especially when revegetated with regional seed mixtures, terraced vineyards have high biodiversity potential and help to reconcile viticulture on steep slopes and nature conservation objectives.

8.1 Evaluating different vineyard types and landscape effects on biodiversity in the UMRV - a synthesis

Local vineyard management and soil conditions differently affected plant, Orthoptera, wild bee and spider species richness, as well as their abundances and community composition. Species-specific requirements such as diet breadth, reproduction and dispersal ability determined species and community responses to local environmental and landscape factors.

Distinct management regimes and disturbance intensities in the two managed vineyard types and fallows shaped local plant diversity, composition, and vegetation structures. Actively managed vineyards (vertically oriented and terraced) had a higher proportion of herbaceous vegetation and open bare ground, while succession on fallow land years after abandonment produced dense shrubby and woody vegetation with sporadic trees. The transition from herbaceous vegetation in managed vineyards to shrubby vegetation with woody elements in vineyard fallows determined community turnover for spiders and plant species. In contrast, Orthoptera were almost absent in fallows and wild bee communities did not cluster in relation to vineyard types but according to their nesting requirements.

Extensive vegetation management on terrace embankments together with a lower nitrogen availability fostered a high plant diversity evident in a mixture of grasses and herbs, annuals and perennials, and taller vegetation, which benefited Orthoptera (Ensifera). Even though flower and herbaceous richness were higher on embankments compared to vertically oriented vineyards and fallows, there was no direct positive effect on wild bees as observed in vineyard inter-rows (Peris-Felipo et al. 2021; Kratschmer et al. 2018; Kehinde and Samways 2014). This phenomenon is known from flower strips

that have stronger effects in simplified agricultural landscapes compared to structurally complex ones, where ecological contrasts introduced by floral resources are not sufficient to result in strong effects (Scheper et al. 2013). Nevertheless, embankments were observed to provide nesting sites for ground-nesting bees and regionally endangered birds. Embankment architecture (steep inclination, high insolation) supported thermophilic spiders in line with findings from terraced vineyards in the Czech Republic (Košulič et al. 2014; Košulič and Hula 2013).

In comparison, structures in vertically oriented vineyards were less favourable habitats. Regular mulching and high vehicular disturbance favoured ruderal and annual plants in open inter-rows, and a grass-dominated sward in vegetated inter-rows that fostered the dominance of single generalistic Orthoptera (Caelifera) and more common and ruderal spider species (e.g. disturbance-tolerant sheet web weavers). However, open inter-rows in terraced and vertically oriented vineyards provided habitats that were similarly suitable for open-adapted species (e.g. *Oedipoda* sp. for sun-basking). Ant abundance (bycatch from pitfall sampling) also benefited from the open soil surface and higher soil temperatures, both favourable for ant nesting (Caprio et al. 2015).

Increasing within-field heterogeneity by alternating management in vineyard inter-rows has recently been proposed to support biodiversity in vineyards (Blaise et al. 2022; Brambilla and Gatti 2022) and might have positive outcomes in intensively managed vineyard landscapes by providing some structural heterogeneity in the monotonous surroundings. However, in the small-structured landscape of the study area, the effects of alternating management in vertically oriented vineyards were marginal.

While active management in vineyards was favourable for many species, woody and undisturbed fallows substantially contributed to species diversity, too. For example, rare and disturbance-sensitive spider species were abundant in fallows. For wild bees, fallows provided essential floral (e.g. flowering of *Crataegus* sp. in spring) and non-floral resources and were of major importance as nesting sites for above-ground nesting bees. In addition, woody structures of fallows likely have high conservation value for other species groups like birds (Assandri et al. 2017; Pithon et al. 2016). Likewise, abandoned traditional orchards provided additional resources (Paz et al. 2023), and in a meta-analysis abandoned orchards and vineyards proved to be valuable habitats for several taxonomic groups and significantly contributed to enhancing β - and γ -diversity (Katayama et al. 2019).

The key role of habitat diversity at the landscape scale through the amount of semi-natural habitats such as grasslands, forests, and hedgerows for biodiversity in vineyard ecosystems is widely acknowledged (e.g. Uzman et al. 2020; Kratschmer et al. 2019; Rosas-Ramos et al. 2019; Assandri et al. 2018). From the arthropods investigated in this study, responses to landscape composition and configuration were not consistent but again contrasting. For overall bee species richness and above

ground-nesting bees, the proximity and cover of SNHs (mainly composed of vineyard fallows) were significant because woody elements are highly valuable resource providers for this group (Bertrand et al. 2019; Garratt et al. 2017). In contrast, Orthoptera which are well-known indicators for open habitats (Matenaar et al. 2015), were tied to open and herbaceous structures (Helbing et al. 2014; Fartmann et al. 2012). For spider and ground hunter abundance, responses to SNH cover were negative and positive to forest proximity, but responses were generally not as pronounced as for bees and were suggested to be diluted by the overall high compositional heterogeneity (Tscharntke et al. 2005). Open habitats provided by vineyard management and expressed as vineyard cover revealed a positive response of Orthoptera communities, above-ground nesting, ground nesting and threatened bees, and underline the necessity for vineyard management for some species.

In summary, vineyard management and the presence of abandoned vineyards maintained across a traditional vineyard agroecosystem supported functionally important groups of plants, herbivores, pollinators and predators. While the management of the vineyards and especially the terraced vineyards clearly supported plant and Orthoptera diversity, there was no difference between vineyard types for spiders, whereas wild bee species richness was higher in fallows. These contrasting and species-specific responses to vineyard types emphasize the importance of habitat and management diversity to meet the many distinct needs. Hence, there is no simple conclusion because different species and species groups are associated with different vineyard characteristics and a change in management regime that benefits the diversity of one group may reduce the diversity of another (Fahrig et al. 2015). Within the framework of this thesis, it became evident that trait-based and species-specific considerations are needed to reveal patterns and derive management recommendations. Importantly, as species have contrasting needs and exploit different habitats and resources, the successful management of viticultural landscapes requires both, active vineyard management and undisturbed (abandoned) sites in spatially connected patches.

Given the progressive abandonment of steep slope viticulture, the conservation significance of viticultural management for the maintenance of vineyard-specific biodiversity remains. Even though abandoned vineyards provided valuable habitats and alternative resources, they do not substitute vineyard management but rather contribute to enhancing γ -diversity. Contrasting the species pool of managed vineyards and fallows, it becomes evident that some of the species solely occurred on managed sites (e.g. 25% of spider species) and would most likely disappear if vineyard management on steep slopes was abandoned completely. Especially for wild bees, many threatened and thermophilic species are associated with vineyards like the monolectic and endangered *Systropha planidens* that is specialized on *Convolvulus arvensis* stocks growing in vineyards (Westrich 2019). From a conservationist's perspective, both elements of active, environmentally friendly vineyard management

(land-sharing) and undisturbed abandoned vineyards (land-sparing) should be well balanced to maintain and preserve the rich biodiversity associated with this traditional cultural landscape.

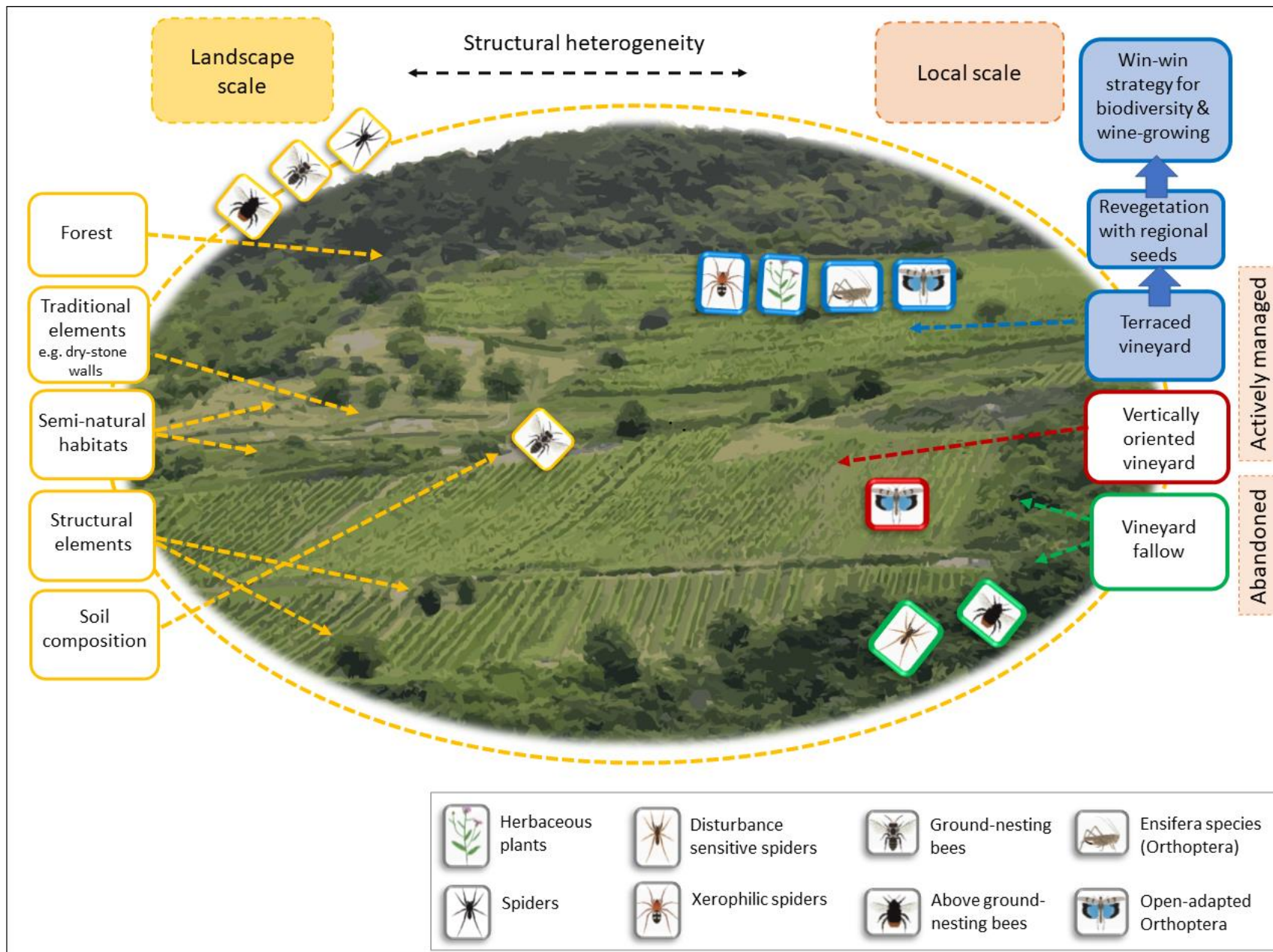


Figure 30: Responses to vineyard types and landscape elements were group and taxon-specific and are indicated by species icons framed with respective colors. The small-structured landscape of the UMRV supported high species diversity and diverse species communities across the three studied vineyard types. Terraced vineyards revealed high biodiversity potential, especially when embankments are revegetated with regional seed mixtures. Species icons by C. Reiß.

8.2 Terracing in steep slope viticulture – ecological potential and research perspectives

Given the ongoing abandonment of steep slope viticulture, one main objective of this thesis was to evaluate the potential of vineyard terracing to promote biodiversity in vineyard ecosystems. As discussed above, terraced vineyards proved to be valuable habitats that created high within-field heterogeneity with a long environmental gradient from open and regularly disturbed terrace inter-rows and extensively managed embankments. As rather nutrient-poor and undisturbed elements are scarce in agricultural landscapes today (Stevens et al. 2010), embankments have enormous potential to support high biodiversity within the agricultural system. Results from chapters 3 and 7 indicate that by adjusting cutting regimes and by initially choosing locally adapted and species-rich seed mixtures, the habitat quality of embankments could even be increased. Due to their lateral expansion, embankments might improve habitat connectivity within viticultural landscapes which is crucial for species survival (Concepción et al. 2020). As previous research has reported the benefits of linear landscape elements in vineyard landscapes such as hedgerows and tree rows for birds (Guyot et al. 2017; Assandri et al. 2016) and arthropods (Duso et al. 2004), it is likely that embankments facilitate species movements within the vineyard landscape, but further investigation would be needed to prove this hypothesis.

Diversifying habitat, feeding and nesting resources in agricultural systems increases the taxonomic richness, functional diversity and abundance of natural enemies and thus enhances natural pest control services (Ostandie et al. 2021; Crowder and Jabbour 2014). In particular, increased plant diversity favours a large diversity of predators like spiders, harvestmen, lacewings, birds and bats in vineyards (Blaise et al. 2022; Charbonnier et al. 2021; Papura et al. 2020; Thiéry et al. 2018). Given this high plant species richness and structural diversity, embankments might contribute to enhancing natural pest control. On the other hand, it is unclear to what extent pesticide drift affects embankments and how that affects arthropods colonizing embankments. Fungicides like sulfur and copper are frequently applied in vineyards and negatively affect arthropod species including pests and their natural enemies (Reiff et al. 2023; Reich et al. 2021; Pennington et al. 2018; Geiger et al. 2010). To reduce the hazardous effects of fungicide applications on arthropods the cultivation of fungus-resistant grape varieties is a promising approach (Reiff et al. 2023). Therefore, the natural pest control potential and the effects of pesticides on embankments should be the subject of future research. In addition, the use of fungus-resistant grape varieties on terraced vineyards should be considered for more sustainable viticulture.

Terraced vineyards contribute to erosion mitigation, which is a major concern in steep slope viticulture (Rodrigo-Comino et al. 2019) and can have disastrous consequences as the flood disaster in the Ahr valley 2021 has shown. Newly constructed embankments are most sensitive to erosion when the vegetative cover is still scarce but regional mixtures and hydro-seeding provided a sufficient vegetation cover. In contrast, non-locally adapted seed mixtures and manual seeding had a higher failure risk and

were more prone to environmental impacts such as severe precipitation events and drought. However, the erosion risk appeared to be inherently lower for newly planted terraced vineyards compared to vertically oriented ones (personal observation within the project). In addition, vineyard terracing reduces the slope length and thus contributes to erosion prevention.

Facing climate change, water scarcity and drought stress gain in significance and water competition between vines and vegetation is a concern many practitioners have (Garcia et al. 2018). Even though water infiltration during winter precipitation is higher for terraced vineyards compared to vertically oriented vineyards, Strack and Stoll (2022) suggested that embankment vegetation exacerbated the water stress of young and not fully adapted vines. However, the interaction between embankment vegetation and vines remains unclear and needs further investigation.

More and more winegrowers recognize that biodiversity and viticulture do not necessarily exclude each other and that advocating sustainability and nature conservation can be a useful marketing tool (Lamoureux et al. 2022; Viers et al. 2013). However, harvesting high-quality grapes with sufficient yields is still the top priority for winegrowers, and there are still many trade-offs between biodiversity and productivity (Grass et al. 2021). Results from the viticulture investigations in this project suggest that site characteristics, variety and age of the vines and the winegrowers' individual management have a stronger influence on vine qualities and berry components than the vineyard management type (Strack and Stoll 2021). On that account, vineyard terracing allows combining wine growing and habitat provision and manages to overcome the trade-off between productivity and biodiversity conservation.

Despite the many advantages, investment costs for constructing terraces are high and might be an obstacle as public subsidies only marginally cover costs (Strub and Loose 2021b). In addition, hydro-seeding of embankments with regional seeds and subsequent management of embankment vegetation (regular mowing, biomass removal) requires investments (e.g. tools for mowing) and additional workload. To date, these services are based on the intrinsic motivation of individual winegrowers. However, vineyard terracing appears to be a win-win strategy for both winegrowers and biodiversity and thus represents a prime example of a land-sharing approach. As such, embankment vegetation management should be subsidized by their implementation into agri-environmental schemes to foster valuable biodiversity measures for sustainable and environmentally friendly viticultural management.

8.3 Beyond grape production

Designing multifunctional vineyard agroecosystems that simultaneously provide a wealth of cultural, ecological and economic services and create synergies between agricultural production and biodiversity conservation remains both a major challenge and a major opportunity (Candiago et al. 2022; Winkler et al. 2017; Viers et al. 2013). To face these complex interactions, holistic thinking and multidisciplinary knowledge are needed to support transformative pathways towards more sustainable agricultural systems (Candiago et al. 2022; Byrnes et al. 2014). For vineyard landscapes, Viers et al. (2013) proposed the concept of ‘vinecology’ where ecological and viticultural practices are coupled in an integrated matrix of natural habitats and crops that yield sustainable economic income and preserve the environment. In this context, communicating nature conservation practices and the values of biodiversity to consumers can be a useful tool as wine grapes are a high-value crop that provides many opportunities for strong consumer engagement (Lamoureux et al. 2022). In the wine industry, interacting with customers, sharing insights about the production, and building a strong relationship with the customers is important (Byrd et al. 2016). Studies show that consumers increasingly value environmental responsibility and are willing to pay higher prices for wines addressing biodiversity and conservation practices in vineyards (Ruggeri et al. 2020; Mazzocchi et al. 2019). Moreover, the quality of a landscape and its natural environment has a major influence on the destination’s attractiveness and are the main reasons for choosing a wine region for touristic activities (Lamoureux et al. 2022).

In most steep slope wine-growing regions, there is a lack of integrative approaches and marketing strategies that simultaneously address the mutual relationships between viticulture, biodiversity, and the preservation of the cultural landscape. Winegrowers, tourism associations, nature conservation associations and other local stakeholders should team up to develop a joint approach and a common trademark that communicates the significance of maintaining vineyards on steep slopes for biodiversity and the cultural heritage.

Summarizing, multiple studies have demonstrated how agrobiodiversity in vineyards and vineyard landscapes can be supported and recommendations for winegrowers are available even though management effects are dependent upon the region and target species (e.g. reviewed by Paiola et al. 2020, Winter et al. 2018). While for steep slopes maintaining management is crucial and vineyard terracing can be a valuable approach for preserving a diverse species pool, on flat-terrain and intensively managed vineyard sites, management rather impairs than supports biodiversity. Here, adopting environmentally friendly farming practices, increasing plant diversity within fields and implementing woody structures represent only some of the measures possible (e.g. Brambilla and Gatti 2022). The evidence gathered in this work and numerous other studies underline that the structural

diversity of vineyard landscapes is a key factor in promoting agrobiodiversity and can even determine the success of locally applied practices (Beaumelle et al. 2021; Uzman et al. 2020).

Scientists have proposed a variety of strategies and individual measures to halt the decline of biodiversity in agricultural landscapes. Key principles include habitat connectivity, heterogeneity and the preservation and restoration of semi-natural and small-landscape elements in combination with regional measures that increase within-field heterogeneity and crop diversification (Concepción et al. 2020; Sirami et al. 2019; Díaz and Concepción 2016). In other words, the knowledge to prevent further biodiversity loss and move towards more sustainable agriculture is already available, but action needs to be taken quickly (Samways et al. 2020). The fate of agrobiodiversity should not depend on the voluntariness and commitment of individual farmers but should be a societal and political decision. Farmers integrating nature conservation need sufficient financial compensation because they are not only preserving biodiversity but also human livelihood. The protection of future agrobiodiversity is highly dependent on the orientation of agricultural policy and subsidies (Pe'er et al. 2022; Pe'er and Lakner 2020). Therefore, the Common Agricultural Policy should allocate a sufficient budget for biodiversity conservation and set more ambitious targets.

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List of Abbreviations

AES	Agri-environment schemes
agg.	Aggregate, grouping of closely-related species
AICc	Akaike information criterion with correction for small sample sizes
CAP	Common agricultural policy
cf.	confer/conferatur, meaning compare
DCA	Detrended Correspondence Analysis
EFA	Ecological focus area
GIS	Geographic Information System
GLM	Generalized linear model
GLMM	Generalized linear mixed effect model
LMM	Linear mixed effect model
n.s.	not significant
PCA	Principal component analysis
R ²	Coefficient of determination
RDA	Redundancy analysis
SE	Standard error
SNH	Semi-natural habitat
sp.	Species (singular), specimen has not been identified to the species level
UMRV	Upper Middle Rhine Valley
VIF	Variance inflation factor

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Statutory Declaration

"I declare that this dissertation has been written solely by myself and without unauthorized external aid, except where explicitly stated in the dissertation. All text passages taken verbatim or mutatis mutandis from published writings and all statements based on oral information are clearly referenced as such.

In the studies carried out and mentioned in the dissertation, I have adhered to the principles of scientific integrity in accordance with the statutes to ensure good scientific practice of Hochschule Geisenheim University and RPTU Kaiserslautern Landau.

§ 16(2) Doctoral regulations of Hochschule Geisenheim University (2018)

Geisenheim, 20th June 2023 _____

Vera Wersebeckmann

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*„Which is more important“ asked Big Panda, „The journey or the destination?“
„The company.“ said Tiny Dragon.*

James Norbury (Big Panda and Tiny Dragon)

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Appendices

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Appendix A – Chapter 3

Table A. 1: Number of records of plant species in vertically oriented vineyards, terraced vineyards, and vineyard fallows sorted by family. Nomenclature follows Buttler et al. (2018). Entries without code were not included in the analysis of species richness or community composition, because they were not reliably determinable. Status of conservation concern is given according to the Red List of Plants in Germany (Metzing et al. 2018) with endangered species highlighted in grey.

Species	Code	Vertically oriented		Terrace		Fallow	Total	Status
		Vegetated Inter-row	Open Inter-row	Embankment	Terrace Inter-row			
Aceraceae								
<i>Acer campestre</i> L.	Ace.cam			1		3	4	
Alliaceae								
<i>Allium rotundum</i> L.	All.rot			1			1	3
<i>Allium vineale</i> L.	All.vin			7	1		8	
Amaranthaceae								
<i>Amaranthus retroflexus</i> L.	Ama.ret	1	5		17		23	
Apiaceae								
<i>Carum carvi</i> L.	Car.car			3	1		4	
<i>Daucus carota</i> L.	Dau.car	20	22	32	31	3	108	
<i>Falcaria vulgaris</i> Bernh.	Fal.vul	3	2	5	1		11	
<i>Foeniculum vulgare</i> Mill.	Foe.vul		2				2	
<i>Peucedanum officinale</i> L.	Peu.off					2	2	3
<i>Torilis japonica</i> (Houtt.) DC.	Tor.jap	7	5	13	6	2	33	
Araliaceae								
<i>Hedera helix</i> L.	Hed.hel			1		4	5	
Asteraceae								
<i>Achillea millefolium</i> L.	Ach.mil	22	8	27	15	1	73	
<i>Anthemis tinctoria</i> L.	Ant.tin	4	1	7		2	14	
<i>Artemisia absinthium</i> L.	Art.abs			3	2		5	
<i>Artemisia vulgaris</i> L.	Art.vul		1	1			2	
<i>Calendula officinalis</i> L.	Cal.off				1		1	
<i>Centaurea cyanus</i> L.	Cen.cya		1	2	3		6	
<i>Centaurea jacea</i> L.	Cen.jac			4	1		5	
<i>Cichorium intybus</i> L.	Cic.int	4	1	1	1		7	
<i>Cirsium arvense</i> (L.) Scop.	Cir.arv	2	3	7	6	2	20	
<i>Cirsium vulgare</i> (Savi) Ten.	Cir.vul	1		2			3	

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<i>Crepis capillaris</i> (L.) Wallr.	Cre.cap	2	3	1	1		7
<i>Echinops sphaerocephalus</i> L.	Ech.sph			2		2	4
<i>Erigeron annuus</i> (L.) Desf	Eri.ann	13	6	8	10		37
<i>Hieracium pilosella</i> L.	Hie.pil	1	1	1		3	6
<i>Inula conyzae</i> (Griess.) DC.	Inu.con			3		1	4
<i>Lactuca perennis</i> L.	Lac.per					1	1
<i>Lactuca serriola</i> L.	Lac.ser	5	11	31	13		60
<i>Leucanthemum ircutianum</i> Turcz. ex DC.	Leu.irc			5			5
<i>Senecio inaequidens</i> DC.	Sen.ina		2	8	2		12
<i>Senecio vulgaris</i> L.	Sen.vul	14	19	4	14		55
<i>Solidago canadensis</i> L.	Sol.can					2	2
<i>Sonchus arvensis</i> L.	Son.arv	1	1				2
<i>Sonchus asper</i> (L.) Hill	Son.asp	4	2		10		16
<i>Sonchus oleraceus</i> L.	Son.ole		1		2		3
<i>Tanacetum vulgare</i> L.	Tan.vul	3	2	26	7	9	47
<i>Taraxacum</i> sect. <i>ruderalia</i> Kirschner, H. Øllg. & Štěpánek	Tar.rud	18	13	6	9		46
<i>Tragopogon dubius</i> Scop.	Tra.dub			4			4
<i>Tripleurospermum perforatum</i> (Mérat) M. Laínz	Tri.per			1			1
Berberidaceae							
<i>Mahonia aquifolium</i> (Pursh) Nutt.	Mah.aqu					1	1
Betulaceae							
<i>Betula pendula</i> Roth	Bet.pen					1	1
<i>Carpinus betulus</i> L.	Car.bet					3	3
Boraginaceae							
<i>Echium vulgare</i> L.	Ech.vul	3	1	16	9	2	31
<i>Myosotis arvensis</i> (L.) Hill	Myo.arv			5			5
Brassicaceae							
<i>Alliaria petiolata</i> (M. Bieb.) Cavara & Grande	All.pet					1	1
<i>Arabidopsis thaliana</i> (L.) Heynh.	Ara.tha	2	1	3	4		10
<i>Brassica napus</i> L.	Bra.nap				1		1
<i>Capsella bursa-pastoris</i> (L.) Medik.	Cap.bur	1	6	1	10		18
<i>Cardamine hirsuta</i> L.	Car.hir	18	15	14	14	2	63
<i>Diplotaxis tenuifolia</i> (L.) DC	Dip.ten	9	13	20	19		61
<i>Draba verna</i> L.	Dra.ver	4	8	8	11	1	32
<i>Isatis tinctoria</i> L.	Isa.tin	4	3	11	2	3	23
<i>Lepidium campestre</i> (L.) R. Br.	Lep.cam	2	5	2	5		14

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<i>Lepidium draba</i> L.	Lep.dra	5	4	8		1	18
<i>Lepidium graminifolium</i> L.	Lep.gra	2	3		2		7
<i>Lepidium sativum</i> L.	Lep.sat	5	4	4	3		16
<i>Raphanus raphanistrum</i> L.	Rha.rha		2				2
<i>Sinapis arvensis</i> L.	Sin.arv	2	2	4	10		18
<i>Sisymbrium officinale</i> (L.) Scop.	Sis.off	2	1	5	1		9
<i>Thlaspi arvense</i> L.	Thl.arv	5	3	3	2		13
Campanulaceae							
<i>Campanula rapunculus</i> L.	Cam.rap	1					1
<i>Campanula rotundifolia</i> L.	Cam.rot					1	1
Caprifoliaceae							
<i>Sambucus nigra</i> L.	Sam.nig			1		2	3
Caryophyllaceae							
<i>Cerastium holosteoides</i> Fr.	Cer.hol	14	15	8	17		54
<i>Holosteum umbellatum</i> L.	Hol.umb	4	3	6	6		19
<i>Silene dioica</i> (L.) Clairv.	Sil.dio			2			2
<i>Silene vulgaris</i> (Moench) Garcke	Sil.vul	2	1	5			8
<i>Stellaria graminea</i> L.	Ste.gra			1			1
<i>Stellaria media</i> (L.) Vill.	Ste.med	10	11	4	11		36
Chenopodiaceae							
<i>Chenopodium album</i> L.	Che.alb	2	6	2	15		25
Clusiaceae							
<i>Hypericum perforatum</i> L.	Hy.per	5	2	11	1	5	24
Convolvulaceae							
<i>Convolvulus arvensis</i> L.	Con.arv	11	11	13	19		54
Cornaceae							
<i>Cornus mas</i> L.	Cor.mas			2		12	14
Crassulaceae							
<i>Sedum album</i> L.	Sed.alb	1	2	2		5	10
Cucurbitaceae							
<i>Bryonia dioica</i> Jacq.	Bry.dio			4		2	6

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Dipsacaceae

<i>Dipsacus fullonum</i> L.	Dip.ful			1			1
<i>Dipsacus sativus</i> (L.) Honck.	Dip.sat					1	1
<i>Knautia arvensis</i> (L.) Coult.	Kna.arv			2			2

Euphorbiaceae

<i>Euphorbia cyparissias</i> L.	Eup.cyp			1		1	2
<i>Euphorbia helioscopia</i> L.	Eup.hel	1	3	1	2		7
<i>Mercurialis annua</i> L.	Mer.ann	10	14	4	19		47

Fabaceae

<i>Anthyllis vulneraria</i> L.	Ant.vul				1		1
<i>Lathyrus latifolius</i> L.	Lat.lat					1	1
<i>Lens culinaris</i> Medik.	Len.cul	6	13	10	15	2	46
<i>Lotus corniculatus</i> L.	Lot.cor			1	1		2
<i>Medicago lupulina</i> L.	Med.lup	2	1	3	1		7
<i>Medicago sativa</i> L.	Med.sat	13	8	6	11		38
<i>Melilotus officinalis</i> (L.) Lam.	Mel.off			1			1
<i>Onobrychis viciifolia</i> Scop.	Ono.vic	1			2		3
<i>Ononis repens</i> L.	Ono.rep	1	1				2
<i>Ononis spinosa</i> L.	Ono.spi			3			3
<i>Robinia pseudoacacia</i> L.	Rob.pse					4	4
<i>Securigera varia</i> (L.) Lassen	Sec.var	2		2			4
<i>Trifolium dubium</i> Sibth.	Tri.dub	6	5		7		18
<i>Trifolium pratense</i> L.	Tri.pra	1	2	2			5
<i>Trifolium repens</i> L.	Tri.rep	4	2		5		11
<i>Vicia angustifolia</i> L.	Vic.ang	1		1			2
<i>Vicia sativa</i> agg.	Vic.sat		1	2	1		4
<i>Vicia tenuifolia</i> Roth	Vic.ten		1	1			2
<i>Vicia tetrasperma</i> (L.) Schreb.	Vic.tet	2	4	8	5		19

Fagaceae

<i>Quercus robur</i> L.	Que.rob					5	5
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Fumariaceae

<i>Fumaria officinalis</i> L.	Fum.off	2	4	8		1	15
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Geraniaceae

<i>Erodium cicutarium</i> (L.) L'Hér.	Ero.cic	12	9	4	28		53
<i>Geranium columbinum</i> L.	Ger.col		1				1
<i>Geranium molle</i> L.	Ger.mol	8	8	6	5	1	28

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<i>Geranium pusillum</i> L.	Ger.pus			2		1		3
<i>Geranium robertianum</i> L.	Ger.rob	2	2					4
<i>Geranium rotundifolium</i> L.	Ger.rot	11	13	11		25	3	63
Hydrophyllaceae								
<i>Phacelia tanacetifolia</i> Benth.	Pha.tan		2	3				5
Lamiaceae								
<i>Lamium album</i> L.	Lam.alb	1	1					2
<i>Lamium purpureum</i> L.	Lam.pur	21	21	18		21		81
<i>Origanum vulgare</i> L.	Ori.vul	1	1	7		1	4	17
<i>Salvia pratensis</i> L.	Sal.pra			6		1		7
<i>Thymus pulegioides</i> L.	Thy.pul			1				1
Malvaceae								
<i>Malva moschata</i> L.	Mal.mos	2						2
<i>Malva neglecta</i> Wallr.	Mal.neg	4	5	1		3		13
<i>Malva sylvestris</i> L.	Mal.syl	8	7	7		8		30
Onagraceae								
<i>Epilobium ciliatum</i> Raf.	Epi.cil		1					1
<i>Epilobium cf. tetragonum</i>		2	2			1		5
Papaveraceae								
<i>Papaver rhoeas</i> L.	Pap.rho	2	2	12		3		19
Plantaginaceae								
<i>Plantago lanceolata</i> L.	Pla.lan	2	2			5		9
<i>Plantago media</i> L.	Pla.med	2				3		5
Poaceae								
<i>Agrostis capillaris</i> L.	Agr.cap	2		6		1		9
<i>Alopecurus pratensis</i> L.	Alo.pra					2		2
<i>Anthoxanthum odoratum</i> L.	Ant.odo	3		3				6
<i>Arrhenatherum elatius</i> (L.) J. Presl & C. Presl	Arr.ela	19	16	39		14	5	93
<i>Bromus erectus</i> Huds.	Bro.ere			15		1		16
<i>Bromus hordeaceus</i> L.	Bro.hor			1				1
<i>Bromus sterilis</i> L., nom. cons.	Bro.ste	4	8	8		4		24
<i>Cynosurus cristatus</i> L.	Cyn.cri			1				1
<i>Dactylis glomerata</i> L.	Dac.glo	5	3	4		5	1	18

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<i>Elymus repens</i> (L.) Gould	Ely.rep	20	11	15	12	2	60
<i>Festuca rubra</i> agg.	Fes.rub	12	4	27	7	3	53
<i>Holcus lanatus</i> L.	Hol.lan		3	3	1		7
<i>Hordeum murinum</i> L.	Hor.mur	8	2		2	1	13
<i>Lolium perenne</i> L.	Lol.per	27	13	4	20		64
<i>Melica transsilvanica</i> Schur, nom. cons.	Mel.tra			2			2 V
<i>Phleum pratense</i> L.	Phl.pra			1			1
<i>Poa annua</i> L.	Poa.ann	4	5	1	27		37
<i>Poa pratensis</i> L.	Poa.pra	1					1
<i>Poa trivialis</i> L.	Poa.tri	5	2	5	4	1	17
<i>Setaria pumila</i> (Poir.) Roem. & Schult.	Set.pum	2	2	2	3	1	10
<i>Vulpia myuros</i> (L.) C. C. Gmel.	Vul.myu			1			1
Polygonaceae							
<i>Polygonum aviculare</i> L.	Pol.avi		3		2		5
<i>Rumex crispus</i> L.	Rum.cri	4	4	4	12	1	25
Primulaceae							
<i>Anagallis arvensis</i> L.	Ana.arv	4	6	1	8		19
<i>Primula veris</i> L.	Pri.ver	1		1			2
Ranunculaceae							
<i>Clematis vitalba</i> L.	Cle.vit	1	1	6		8	16
<i>Ranunculus repens</i> L.	Ran.rep	8	5	1	20		34
Resedaceae							
<i>Reseda lutea</i> L.	Res.lut	2		2			4
<i>Reseda luteola</i> L.	Res.lute	3	3		1		7
Rosaceae							
<i>Crataegus laevigata</i> (Poir.) DC.	Cra.lae			2		14	16
<i>Crataegus monogyna</i> Jacq.	Cra.mon					1	1
<i>Fragaria vesca</i> L.	Frau.ves	3	2	2		2	9
<i>Geum urbanum</i> L.	Geu.urb	8	7	1	2	1	19
<i>Potentilla argentea</i> L.	Pot.arg					2	2
<i>Potentilla reptans</i> L.	Pot.rep	9	4	2	2	1	18
<i>Prunus avium</i> (L.) L.	Pru.avi			1		18	19
<i>Prunus domestica</i> L.	Pru.dom					1	1
<i>Prunus mahaleb</i> L.	Pru.mah					16	16
<i>Rosa canina</i> agg.	Ros.can	5	3	13		29	50
<i>Rubus fruticosus</i> agg.	Rub.fru	7	7	37	7	29	87

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<i>Sanguisorba minor</i> Scop.	San.min	3	2	2	2	9
Rubiaceae						
<i>Galium album</i> Mill.	Gal.alb	16	7	39	16	90
<i>Galium aparine</i> L.	Gal.apa		3	14	4	21
<i>Galium verum</i> L.	Gal.ver	3		17	1	26
Salicaceae						
<i>Populus tremula</i> L.	Pop.tre				1	1
Scrophulariaceae						
<i>Linaria vulgaris</i> Mill.	Lin.vul	1	1	3	2	7
<i>Verbascum thapsus</i> agg.	Ver.tha	1	1	6	2	10
<i>Veronica arvensis</i> L.	Ver.arv		2	4		6
<i>Veronica hederifolia</i> L.	Ver.hed	15	14	15	12	57
<i>Veronica persica</i> Poir.	Ver.per	19	27	7	20	73
Solanaceae						
<i>Solanum nigrum</i> L.	Sol.nig	1	1		2	4
Urticaceae						
<i>Urtica dioica</i> L.	Urt.dio			2	1	3
Valerianaceae						
<i>Valerianella carinata</i> Loisel.	Val.car			2		2
<i>Valerianella locusta</i> (L.) Laterr.	Val.loc			2		2
Vitaceae						
<i>Vitis vinifera</i> L.	Vit.vin			2	1	3
Total		595	535	843	712	2959

¹ Status of conservation concern with V – near threatened, 3 – endangered

References:

Buttler, K. P.; May, R.; Metzging, D. (2018): Liste der Gefäßpflanzen Deutschlands. Florensynopse und Synonyme. Bonn-Bad Godesberg: Bundesamt für Naturschutz (BfN-Skripten, 519).
 Metzging, D.; Garve, E.; Matzke-Hajek, G.; Adler, J.; Bleeker, W.; Breunig, T. et al.(2018): Rote Liste und Gesamtartenliste der Farn- und Blütenpflanzen (Trachaeophyta) Deutschlands. Bonn Bad Godesberg.

Appendices

Table A. 2: Correlation of environmental and indicator values with the first two DCA components related to plant species composition in vineyard types. Variables that were significantly related to the DCA axes ($p < 0.05$, 9999 permutations) are printed in bold. Asterisks indicate significance levels ($p < 0.05=*$, $p < 0.005=**$, $p < 0.001=***$).

Variable	DCA1	DCA2	Pr (>r)
Vegetation cover [%]	-0.0472	0.9988	0.8970
Bare ground cover [%]	-0.9638	0.2663	0.0160 *
Litter cover [%]	-0.2261	0.9741	0.8090
Shrub cover [%]	0.9868	0.1614	0.0010 ***
Tree cover [%]	0.9906	-0.1366	0.0010 ***
Grass cover [Londo]	-0.8699	-0.4931	0.0010 ***
Herbaceous cover [Londo]	-0.5301	0.8479	0.0010 ***
Ellenberg indicator reaction (IndR)	0.9909	-0.1342	0.0010 ***
Ellenberg indicator light (IndL)	-0.8968	-0.4424	0.0010 ***
Ellenberg indicator temperature (IndT)	0.3909	-0.9204	0.0620
Ellenberg indicator moisture (IndM)	-0.9825	0.1862	0.0380 *
Ellenberg indicator nitrogen (IndN)	-0.9967	0.0805	0.0010 ***
Competitiveness (Comp)	0.9209	0.3897	0.0010 ***
Stress tolerance (Stress)	0.3876	-0.9218	0.8080
Ruderality	-0.9387	-0.3444	0.0010 ***
Annual	-0.8425	-0.5387	0.0010 ***
Biennial	-0.9895	0.1445	0.0020 **
Perennial	0.1351	-0.9908	0.5530

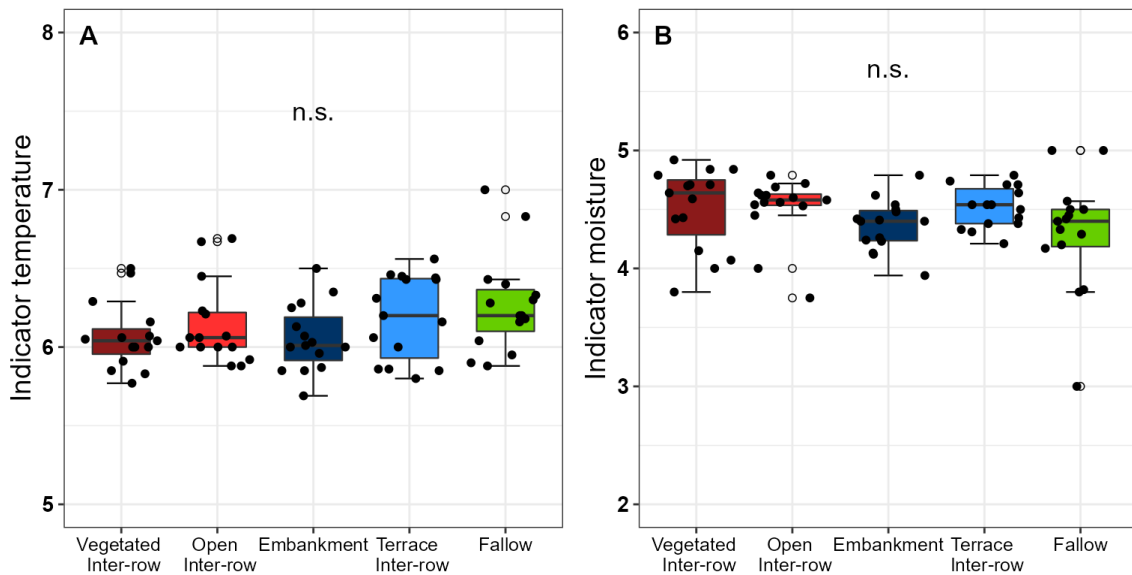


Figure A. 1: Differences in mean Ellenberg indicator values for temperature (A), and moisture (B) between vineyard compartments analyzed using LMMs. Each data point represents the mean value per site for the respective vineyard compartment (N = 15). Non-significant differences are indicated by n.s.

Appendices

Appendix B – Chapter 4

Table B. 1: Abundances of all sampled Orthoptera sorted by family for vineyard types and compartments of vertically oriented vineyards, compartments of terraced vineyards, and canopy. Individuals that were captured in the canopy were not included in the analysis. The status of conservation concern is given according to the Red List for Orthoptera in Germany (Maas et al 2011), with endangered species highlighted in grey.

Species	Code	Vertically oriented			Total	Terrace			Fallow		Status ¹	
		Vegetated Inter-row	Open Inter-row	Canopy		Embankment	Inter-Row	Canopy	Total	Total		
Gomphocerinae												
<i>Chorthippus biguttulus</i>	Cho.big	58	29	0	87	10	15	0	25	0	112	
<i>Chorthippus brunneus</i>	Cho.bru	6	5	0	11	1	6	0	7	0	18	
<i>Chorthippus dorsatus</i>	Cho.dor	0	0	0	0	1	0	0	1	0	1	
<i>Chorthippus vagans</i>	Cho.vag	2	2	0	4	3	0	0	3	0	7	3
<i>Pseudochorthippus parallelus</i>	Pse.par	1	0	0	1	0	0	0	0	0	1	
Gryllidae												
<i>Nemobius sylvestris</i>	Nem.syl	0	0	0	0	1	0	0	1	0	1	
Meconematinae												
<i>Meconema meridionale</i>	Mec.mer	0	0	0	0	1	0	0	1	1	3	
Oecanthinae												
<i>Oecanthus pellucens</i>	Oec.pel	0	1	1	2	13	6	0	19	3	24	
Oedipodinae												
<i>Oedipoda caerulescens</i>	Oed.cae	1	13	0	14	3	15	1	19	0	32	V
<i>Oedipoda germanica</i>	Oed.ger	2	1	0	3	0	0	0	0	0	3	1
Phaneropterinae												
<i>Phaneroptera falcata</i>	Pha.fal	0	0	0	0	3	2	0	5	0	5	
<i>Phaneroptera nana</i>	Pha.nan	0	0	0	0	0	0	0	0	1	2	
Tettigoniinae												
<i>Leptophyes punctatissima</i>	Lep.pun	0	0	1	1	0	0	0	0	1	2	
<i>Pholidoptera griseoaptera</i>	Pho.gri	0	0	0	0	1	0	0	1	0	1	
<i>Platycleis albopunctata</i>	Pla.alb	4	4	0	8	14	1	0	15	0	23	
Total		74	55	2	131	51	45	1	97	6	234	

¹ Status of conservation concern with V – near threatened, 3 – endangered, 1 – threatened with extinction

References (Table B. 1):

Maas, S.; Detzel, P.; Staudt, A. Rote Liste und Gesamtartenliste der Heuschrecken (Saltatoria) Deutschlands. In Rote Liste Gefährdeter Tiere, Pflanzen und Pilze Deutschlands: Band 70 (3): Wirbellose Tiere (Teil 1); Binot-Hafke, M., Balzer, S., Becker, N., Gruttke, H., Haupt, H., Hofbauer, N., Ludwig, G., Matzke-Hajek, G., Strauch, M., Eds.; Bundesamt für Naturschutz: Bonn-Bad Godesberg, Germany, 2011.

Table B. 2: Effects of local vineyard and landscape parameters on Caelifera and Ensifera species richness and density, and density of the two most abundant species *Chorthippus biguttulus* and *Oedipoda caerulescens* analysed using vineyard types. The presented estimates and p-values are obtained from the single models $Y \sim \text{Intercept} + \text{Predictor}$ with 'vineyard triplet' as random factor. R^2 marginal gives explained variation without and R^2 conditional with the random factor. Significant predictors ($p < 0.05$) are printed in bold; SNH: semi-natural habitat.

Dependent variable	Predictor	Estimate \pm SE	p-Value	R^2_{marg}	R^2_{cond}	AICc	
Caelifera species richness	SNH (%)	0.01 \pm 0.14	0.7890	0.01	0.01	140.0	
	Vineyard (%)	-0.18 \pm 0.14	0.1900	0.03	0.03	138.9	
	Forest (%)	0.14 \pm 0.14	0.3310	0.02	0.02	139.7	
	SNH distance (m)	0.11 \pm 0.14	0.4180	0.01	0.00	140.0	
	Forest distance (m)	-0.19 \pm 0.16	0.2350	0.03	0.00	139.1	
	Vegetation height (cm)	-1.15 \pm 0.32	0.0003	0.66	0.66	116.2	
	Bare ground cover (%)	0.38 \pm 0.12	0.0016	0.14	0.14	131.5	
	Vegetation cover (%)	0.19 \pm 0.12	0.1320	0.03	0.03	138.5	
	Shrub cover (%)	-1.21 \pm 0.32	0.0002	0.70	0.70	112.3	
	Litter cover (%)	0.06 \pm 0.14	0.6766	0.01	0.01	140.4	
	Caelifera density	SNH (%)	0.04 \pm 0.05	0.3750	0.02	0.02	33.9
		Vineyard (%)	-0.01 \pm 0.05	0.9710	0.01	0.01	34.7
		Forest (%)	0.01 \pm 0.05	0.9610	0.01	0.01	34.7
		SNH distance (m)	0.03 \pm 0.05	0.4910	0.01	0.00	34.2
Forest distance (m)		-0.03 \pm 0.05	0.5810	0.01	0.00	34.4	
Vegetation height (cm)		-0.14 \pm 0.05	0.0051	0.16	0.22	27.7	
Bare ground cover (%)		0.11 \pm 0.05	0.0352	0.11	0.11	30.5	
Vegetation cover (%)		0.11 \pm 0.05	0.0245	0.10	0.10	29.9	
Shrub cover (%)		-0.14 \pm 0.04	0.0013	0.19	0.21	25.3	
Litter cover (%)		-0.02 \pm 0.05	0.7490	0.01	0.01	34.6	
Ensifera species richness		SNH (%)	-0.13 \pm 0.16	0.1020	0.08	0.08	117.5
		Vineyard (%)	0.31 \pm 0.16	0.0543	0.11	0.11	116.5
		Forest (%)	0.01 \pm 0.17	0.9590	0.01	0.08	120.1
		SNH distance (m)	0.42 \pm 0.14	0.0040	0.18	0.24	113.8
	Forest distance (m)	-0.09 \pm 0.18	0.6260	0.01	0.05	121.8	
	Vegetation height (cm)	-0.54 \pm 0.26	0.0352	0.26	0.33	113.8	
	Bare ground cover (%)	0.22 \pm 0.17	0.2100	0.05	0.20	118.5	
	Vegetation cover (%)	0.17 \pm 0.15	0.2530	0.04	0.05	1118.9	
	Shrub cover (%)	-0.51 \pm 0.23	0.0340	0.24	0.27	114.1	
	Litter cover (%)	0.10 \pm 0.16	0.5240	0.01	0.08	119.7	
	Ensifera density	SNH (%)	-0.04 \pm 0.02	0.0304	0.10	0.10	-45.9
		Vineyard (%)	0.05 \pm 0.02	0.0112	0.13	0.13	-47.5
		Forest (%)	-0.02 \pm 0.02	0.3970	0.02	0.02	-42.2
		SNH distance (m)	0.06 \pm 0.02	0.0029	0.17	0.00	-49.5
Forest distance (m)		0.01 \pm 0.02	0.5510	0.01	0.01	-41.8	
Vegetation height (cm)		-0.02 \pm 0.02	0.3810	0.02	0.02	-42.2	
Bare ground cover (%)		-0.02 \pm 0.02	0.4090	0.02	0.02	-42.1	
Vegetation cover (%)		0.01 \pm 0.02	0.7080	0.01	0.01	-41.6	
Shrub cover (%)		-0.01 \pm 0.02	0.8460	0.01	0.01	-41.5	
Litter cover (%)		0.02 \pm 0.02	0.3730	0.02	0.02	-42.2	

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<i>C. biguttulus</i> density	SNH (%)	-0.01 ± 0.04	0.8194	0.01	0.00	18.8	
	Vineyard (%)	0.05 ± 0.04	0.2624	0.03	0.00	17.7	
	Forest (%)	-0.02 ± 0.04	0.6048	0.01	0.00	18.6	
	SNH distance (m)	0.05 ± 0.04	0.2387	0.03	0.00	17.5	
	Forest distance (m)	0.02 ± 0.04	0.7877	0.01	0.00	18.6	
	Vegetation height (cm)	-0.08 ± 0.04	0.0393	0.09	0.00	14.8	
	Bare ground cover (%)	0.03 ± 0.04	0.4824	0.01	0.00	18.4	
	Vegetation cover (%)	0.09 ± 0.04	0.0192	0.11	0.00	13.7	
	Shrub cover (%)	-0.01 ± 0.02	0.8460	0.01	0.01	41.5	
	Litter cover (%)	0.01 ± 0.04	0.8140	0.01	0.00	18.8	
	<i>O. caerulescens</i> density	SNH (%)	-0.03 ± 0.01	0.0220	0.11	0.00	-83.2
		Vineyard (%)	0.02 ± 0.01	0.1189	0.05	0.00	-80.6
		Forest (%)	-0.01 ± 0.01	0.9068	0.00	0.00	-78.3
SNH distance (m)		-0.01 ± 0.02	0.7040	0.01	0.00	-78.4	
Forest distance (m)		-0.02 ± 0.02	0.1984	0.04	0.00	-79.9	
Vegetation height (cm)		-0.02 ± 0.01	0.1590	0.04	0.00	-80.2	
Bare ground cover (%)		0.05 ± 0.02	<0.0001	0.31	0.00	-94.3	
Vegetation cover (%)		0.01 ± 0.01	0.7396	0.01	0.00	-78.3	
Shrub cover (%)		-0.03 ± 0.01	0.0328	0.09	0.00	-82.6	
Litter cover (%)		-0.03 ± 0.01	0.0591	0.08	0.00	-81.7	

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Table B. 3: Effects of local vineyard and landscape parameters on Orthoptera, Caelifera and Ensifera species richness and density, and density of the two most abundant species *Chorthippus biguttulus* and *Oedipoda caerulescens* analysed using vineyard compartments. The presented estimates and p-values are obtained from the single models $Y \sim \text{Intercept} + \text{Predictor}$ with 'vineyard row' as random factor. R^2 marginal gives explained variation without and R^2 conditional with the random factor. Significant predictors ($p < 0.05$) are printed in bold; SNH: semi-natural habitat.

Dependent variable	Predictor	Estimate \pm SE	p-Value	R^2_{marg}	R^2_{cond}	AICc	
Orthoptera species richness	SNH (%)	0.11 \pm 0.09	0.1830	0.02	0.07	186.5	
	Vineyard (%)	-0.07 \pm 0.09	0.4300	0.01	0.07	187.7	
	Forest (%)	0.12 \pm 0.08	0.1260	0.02	0.07	186.1	
	SNH distance (m)	0.07 \pm 0.08	0.3730	0.01	0.07	187.5	
	Forest distance (m)	-0.14 \pm 0.09	0.1160	0.04	0.07	185.7	
	Vegetation height (cm)	0.18 \pm 0.06	0.0048	0.06	0.10	181.4	
	Bare ground cover (%)	-0.21 \pm 0.08	0.0158	0.07	0.19	182.6	
	Vegetation cover (%)	0.06 \pm 0.08	0.4420	0.01	0.01	187.7	
	Shrub cover (%)	0.07 \pm 0.07	0.3290	0.01	0.09	187.4	
	Litter cover (%)	0.16 \pm 0.08	0.0567	0.04	0.17	184.77	
	Orthoptera density	SNH (%)	0.05 \pm 0.06	0.4010	0.01	0.11	88.3
		Vineyard (%)	0.04 \pm 0.06	0.5370	0.01	0.11	88.6
		Forest (%)	0.06 \pm 0.06	0.3620	0.02	0.11	88.2
SNH distance (m)		0.03 \pm 0.07	0.6420	0.01	0.11	88.8	
Forest distance (m)		-0.04 \pm 0.07	0.5780	0.01	0.11	88.7	
Vegetation height (cm)		0.11 \pm 0.06	0.0710	0.05	0.17	85.8	
Bare ground cover (%)		-0.12 \pm 0.06	0.0477	0.06	0.23	85.3	
Vegetation cover (%)		0.15 \pm 0.06	0.0161	0.09	0.16	83.5	
Shrub cover (%)		0.02 \pm 0.06	0.7040	0.01	0.13	88.9	
Litter cover (%)		0.04 \pm 0.06	0.5700	0.01	0.15	88.7	
Caelifera species richness		SNH (%)	0.31 \pm 0.11	0.0024	0.18	0.00	146.5
		Vineyard (%)	-0.22 \pm 0.09	0.0133	0.10	0.00	150.1
		Forest (%)	0.18 \pm 0.08	0.0161	0.02	0.00	151.0
	SNH distance (m)	-0.13 \pm 0.09	0.1986	0.03	0.00	154.2	
	Forest distance (m)	-0.21 \pm 0.11	0.0734	0.09	0.00	152.4	
	Vegetation height (cm)	0.05 \pm 0.09	0.6037	0.01	0.00	155.7	
	Bare ground cover (%)	-0.06 \pm 0.11	0.5400	0.01	0.03	155.6	
	Vegetation cover (%)	0.09 \pm 0.09	0.2650	0.02	0.03	154.8	
	Shrub cover (%)	-0.01 \pm 0.09	0.9190	0.00	0.03	156.0	
	Litter cover (%)	0.01 \pm 0.09	0.9640	0.00	0.03	156.0	
	Caelifera density	SNH (%)	0.11 \pm 0.06	0.0762	0.06	0.16	77.4
		Vineyard (%)	0.01 \pm 0.06	0.9920	0.00	0.16	80.4
		Forest (%)	0.05 \pm 0.06	0.4590	0.01	0.16	79.8
SNH distance (m)		-0.01 \pm 0.06	0.9680	0.00	0.16	80.4	
Forest distance (m)		-0.03 \pm 0.06	0.5780	0.01	0.16	80.1	
Vegetation height (cm)		0.04 \pm 0.06	0.4710	0.01	0.16	79.9	
Bare ground cover (%)		-0.03 \pm 0.06	0.5990	0.01	0.17	80.1	
Vegetation cover (%)		0.12 \pm 0.06	0.0446	0.07	0.16	76.6	
Shrub cover (%)		0.01 \pm 0.06	0.9910	0.00	0.16	80.4	
Litter cover (%)		-0.04 \pm 0.06	0.5050	0.01	0.15	79.9	
Ensifera species richness		SNH (%)	-0.21 \pm 0.18	0.2390	0.04	0.12	127.2
		Vineyard (%)	0.25 \pm 0.18	0.1565	0.06	0.12	126.2
		Forest (%)	-0.05 \pm 0.19	0.8012	0.01	0.12	128.5
	SNH distance (m)	0.41 \pm 0.15	0.0043	0.19	0.00	123.4	
	Forest distance (m)	-0.06 \pm 0.19	0.7527	0.01	0.26	130.1	
	Vegetation height (cm)	0.41 \pm 0.13	0.0021	0.13	0.20	119.9	
	Bare ground cover (%)	-0.47 \pm 0.20	0.0198	0.16	0.26	122.4	

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	Vegetation cover (%)	-0.02 ± 0.18	0.8931	0.01	0.12	128.5
	Shrub cover (%)	0.17 ± 0.13	0.1888	0.03	0.14	127.1
	Litter cover (%)	0.42 ± 0.18	0.0219	0.13	0.27	122.8
Ensifera density	SNH (%)	-0.03 ± 0.02	0.1670	0.04	0.22	-40.6
	Vineyard (%)	0.03 ± 0.02	0.2090	0.03	0.22	-40.3
	Forest (%)	-0.01 ± 0.02	0.8730	0.01	0.21	-38.8
	SNH distance (m)	0.06 ± 0.02	0.0088	0.12	0.22	-44.9
	Forest distance (m)	0.01 ± 0.03	0.5550	0.01	0.21	-39.1
	Vegetation height (cm)	0.08 ± 0.02	<0.0001	0.24	0.60	-57.4
	Bare ground cover (%)	-0.06 ± 0.02	0.0035	0.11	0.39	-46.4
	Vegetation cover (%)	-0.01 ± 0.02	0.7430	0.01	0.22	-38.8
	Shrub cover (%)	0.03 ± 0.02	0.1250	0.04	0.30	-41.0
	Litter cover (%)	0.06 ± 0.02	0.0018	0.13	0.42	-47.5
<i>C. biguttulus</i> density	SNH (%)	0.02 ± 0.06	0.7270	0.01	0.23	63.7
	Vineyard (%)	0.07 ± 0.06	0.2040	0.03	0.23	62.2
	Forest (%)	-0.01 ± 0.06	0.8530	0.01	0.23	63.8
	SNH distance (m)	0.04 ± 0.06	0.5090	0.01	0.23	63.4
	Forest distance (m)	0.02 ± 0.06	0.6890	0.01	0.23	63.6
	Vegetation height (cm)	0.08 ± 0.05	0.0849	0.04	0.31	60.9
	Bare ground cover (%)	-0.08 ± 0.05	0.1010	0.04	0.27	61.2
	Vegetation cover (%)	0.12 ± 0.05	0.0142	0.11	0.26	58.1
	Shrub cover (%)	0.03 ± 0.05	0.5980	0.01	0.26	63.5
	Litter cover (%)	0.01 ± 0.05	0.8460	0.01	0.24	63.8
<i>O. caerulescens</i> density	SNH (%)	-0.05 ± 0.02	0.0122	0.11	0.00	-51.1
	Vineyard (%)	-0.03 ± 0.02	0.1282	0.04	0.00	-47.4
	Forest (%)	0.03 ± 0.02	0.1317	0.04	0.00	-47.4
	SNH distance (m)	-0.02 ± 0.02	0.3816	0.01	0.00	-45.9
	Forest distance (m)	-0.03 ± 0.02	0.1791	0.03	0.00	-47.0
	Vegetation height (cm)	-0.02 ± 0.02	0.3462	0.02	0.10	-46.1
	Bare ground cover (%)	0.06 ± 0.02	0.0008	0.16	0.00	-55.4
	Vegetation cover (%)	-0.02 ± 0.02	0.4278	0.01	0.00	-48.8
	Shrub cover (%)	-0.03 ± 0.02	0.2147	0.03	0.00	-46.7
	Litter cover (%)	-0.05 ± 0.02	0.0065	0.12	0.00	-52.2

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Table B. 4: Correlation of environmental and landscape variables with the first two DCA components related to Orthoptera species composition in vineyard compartments. Variables that were significantly related to the DCA axes ($p < 0.05$, 9999 permutations) are printed in bold. Asterisks indicate significance levels ($p < 0.05=*$, $p < 0.005=**$); SNH: semi-natural habitat.

Variable	DCA1	DCA2	Pr (>r)
SNH (%)	0.2768	-0.9609	0.0610
Vineyard (%)	-0.6143	0.9981	0.0230 *
Forest (%)	-0.0978	-0.9952	0.3890
SNH distance (m)	-0.1455	0.8943	0.0020 **
Forest distance (m)	0.4476	0.8942	0.4650
Vegetation height (cm)	-0.1116	0.9938	0.2260
Bare ground cover (%)	-0.8813	-0.4727	0.0290 *
Vegetation cover (%)	0.4355	-0.9002	0.4490
Shrub cover (%)	0.4596	0.8879	0.3140
Litter cover (%)	0.6258	0.7800	0.0260 *

Table B. 5: Correlation of environmental and landscape variables with the first two PCA components related to Orthoptera species composition in vineyard types. Variables that were significantly related to the PCA axes ($p < 0.05$, 9999 permutations) are printed in bold. Asterisks indicate significance levels ($p < 0.005=**$); SNH: semi-natural habitat.

Variable	PC1	PC2	Pr (>r)
SNH (%)	0.0842	-0.9965	0.1370
Vineyard (%)	0.4296	0.9030	0.1920
Forest (%)	-0.9833	-0.1823	0.6530
SNH distance (m)	0.8418	0.5398	0.4540
Forest distance (m)	0.4777	0.8785	0.2390
Vegetation height (cm)	-0.5822	-0.8130	0.7890
Bare ground cover (%)	-0.1889	-0.9819	0.0060 **
Vegetation cover (%)	0.9774	0.2113	0.4920
Shrub cover (%)	-0.7962	0.6051	0.0790
Litter cover (%)	0.1444	0.9896	0.0580

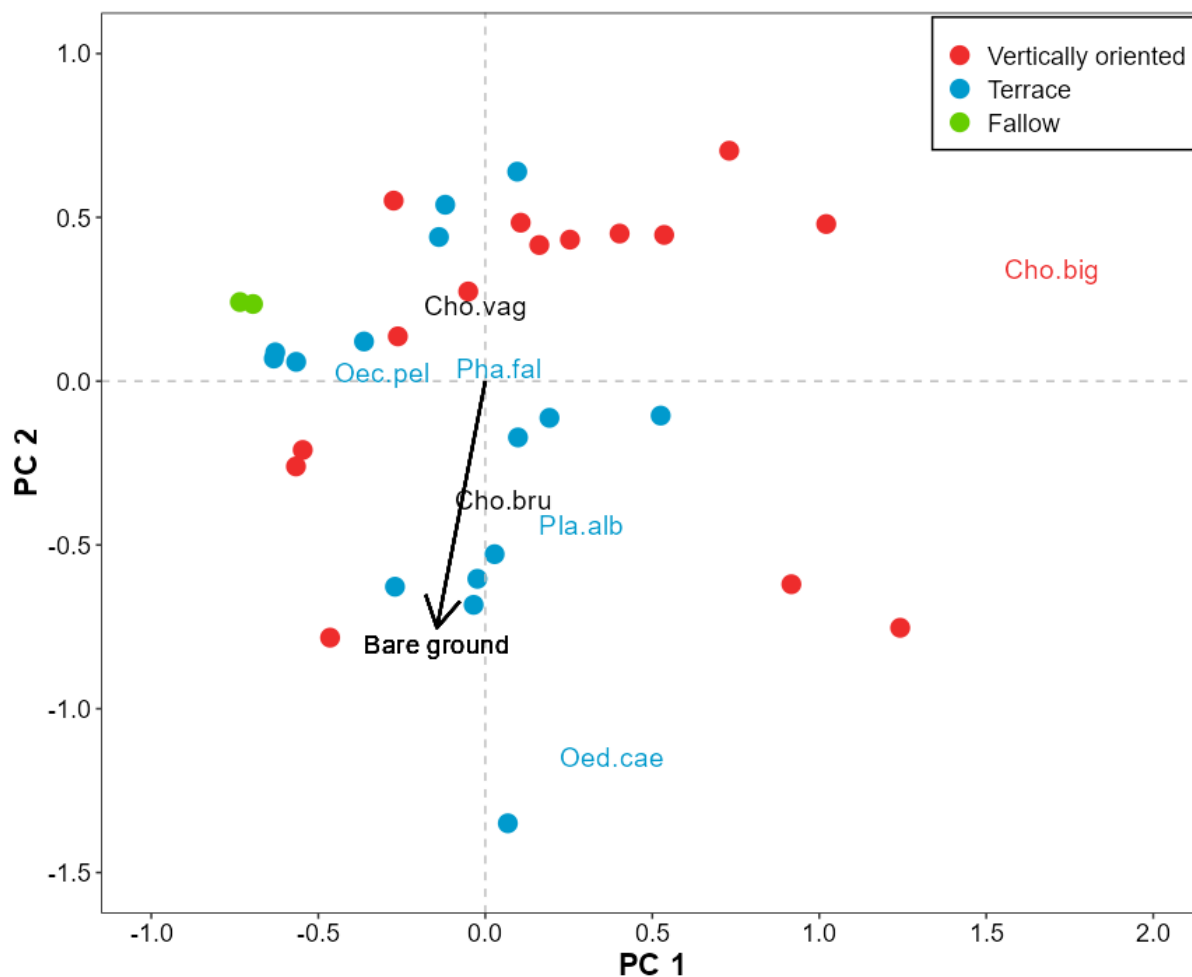


Figure B. 1: PCA results for Orthoptera species composition of vineyard types. The first component explained 38.99 % of variance, the second component 22.28 %. Dots show sample scores for vertically oriented vineyards (red), terraced vineyards (blue) and fallows (green). Environmental and landscape variables that were significantly related to the PCA axes ($p < 0.05$, 9999 permutations) were included post-hoc by projection. Indicator species are coloured in red for vertically oriented vineyards and in blue for terraced vineyards. For black-coloured species names, no assigned indicator values were available. Cho.big: *Chorthippus biguttulus*; Cho.bru: *Chorthippus brunneus*; Cho.vag: *Chorthippus vagans*; Oec.pel: *Oecanthus pellucens*; Oed.cae: *Oedipoda caerulescens*; Pha.fal: *Phaneroptera falcata*; Pla.alb: *Platycleis albopunctata*.

Appendix C – Chapter 5

Table C. 1: Abundance of all sampled wild bees in vertically oriented vineyards, terraced vineyards, and vineyard fallows. Bees were identified by using the determination keys of Amiet et al. (2017,2007, 2004, 2001, 1999) and Schmid-Egger & Scheuchel (1997). Nomenclature follows the checklist of wild bees for Germany (Scheuchel et al. 2018). Entries without code were not included in the analysis of species richness or community composition, because they were not reliably determinable. Status of conservation concern is given according to the Red List for Apidae in Germany (Westrich et al. 2011) with endangered species highlighted in grey.

Species	Code	Vertically oriented	Terrace	Fallow	Total	Status ¹
<i>Andrena bicolor</i> Fabricius, 1775	And.bic	15	4	3	22	
<i>Andrena carantonica</i> Pérez, 1902	And.car	1			1	
<i>Andrena cineraria</i> (Linnaeus, 1758)	And.cin	13	19	63	95	
<i>Andrena combinata</i> (Christ, 1791)	And.com			2	2	3
<i>Andrena curvungula</i> Thomson, 1870	And.cur		1	2	3	3
<i>Andrena dorsata</i> (Kirby, 1802)	And.dor	1		5	6	
<i>Andrena flavipes</i> Panzer, 1799	And fla	67	83	30	180	
<i>Andrena fulva</i> (Müller, 1766)	And.ful	1		1	2	
<i>Andrena gravida</i> Imhoff, 1832	And.gra	4	13	7	24	
<i>Andrena haemorrhoa</i> (Fabricius, 1781)	And.hae	1		2	3	
<i>Andrena hattorfiana</i> (Fabricius, 1775)	And.hat	1			1	3
<i>Andrena helvola</i> (Linnaeus, 1758)	And.hel	1			1	
<i>Andrena labiata</i> Fabricius, 1781	And.lab	1			1	
<i>Andrena lagopus</i> Latreille, 1809	And.lag	18	17	6	41	
<i>Andrena minutula</i> (Kirby, 1802)	And.min	7	4	14	25	
<i>Andrena minutuloides</i> Perkins, 1914	And.minu	2	4	3	9	
<i>Andrena nigroaenea</i> (Kirby, 1802)	And.nig	29	29	14	72	
<i>Andrena nitida</i> (Müller, 1776)	And.nit			2	2	
<i>Andrena nitidiuscula</i> Schenck, 1853	And.niti		1		1	3
<i>Andrena pandellei</i> Pérez, 1895	And.pan		2	3	5	3
<i>Andrena rufula</i> Schmiedeknecht, 1883	And.ruf		3	4	7	
<i>Andrena strohmeilla</i> Stöckhert, 1928	And.str		1	1	2	
<i>Andrena vaga</i> Panzer, 1799	And.nag	1	3	1	5	
<i>Anthophora plumipes</i> (Pallas, 1772)	Ant.plu			1	1	
<i>Bombus barbutellus</i> (Kirby, 1802)	Bom.bar		1	1	2	
<i>Bombus hortorum</i> agg. (Linnaeus, 1761)	Bom.hor			3	3	
<i>Bombus lapidarius</i> (Linnaeus, 1758)	Bom.lap	3		1	4	
<i>Bombus norvegicus</i> (Sparre-Schneider, 1918)	Bom.nor	1			1	
<i>Bombus pascuorum</i> (Scopoli, 1763)	Bom.pas	1	1	1	3	
<i>Bombus pratorum</i> (Linnaeus, 1761)	Bom.pra		1	2	3	
<i>Bombus rupestris</i> (Fabricius, 1793)	Bom.rup	1		3	4	
<i>Bombus terrestris</i> agg. (Linnaeus, 1758)	Bom.ter	3	5	7	15	
<i>Bombus vestalis</i> (Geoffroy, 1785)	Bom.ves			1	1	
<i>Ceratina chalybea</i> Chevrier, 1872	Cer.cha	7	15	27	49	3
<i>Ceratina cucurbitina</i> (Rossi, 1792)	Cer.cur	10	12	16	38	
<i>Ceratina cyanea</i> (Kirby, 1802)	Cer.cya	5	9	19	33	
<i>Chelostoma campanularum</i> (Kirby, 1802)	Che.cam	2	1	7	10	
<i>Chelostoma distinctum</i> (Stöckhert, 1929)	Che.dis	3		2	5	
<i>Chelostoma florissomne</i> (Linnaeus, 1758)	Che.flo			2	2	
<i>Chelostoma rapunculii</i> (Lepeletier, 1841)	Che.rap		1		1	
<i>Colletes cunicularius</i> (Linnaeus, 1761)	Col.cun		3	47	50	
<i>Colletes daviesanus</i> Smith, 1846	Col.dav		1	2	3	
<i>Colletes similis</i> Schenck, 1853	Col.sim		1		1	V
<i>Eucera nigrescens</i> Pérez, 1879	Euc.nig	3	1		4	
<i>Halictus eurygnathus</i> Blüthgen, 1931	Hal.eur	4	6	2	12	
<i>Halictus maculatus</i> Smith, 1848	Hal.mac	30	11	14	55	
<i>Halictus quadricinctus</i> (Fabricius, 1776)	Hal.qua	11	9	5	25	3

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<i>Halictus rubicundus</i> (Christ, 1791)	Hal.rub	1	2	3	6	
<i>Halictus scabiosae</i> (Rossi, 1790)	Hal.sca	21	37	12	70	
<i>Halictus sexcinctus</i> (Fabricius, 1775)	Hal.sex	1			1	3
<i>Halictus simplex</i> agg. Blüthgen, 1923	Hal.sim	46	40	38	124	
<i>Halictus subauratus</i> (Rossi, 1792)	Hal.sub	8	8	2	18	
<i>Halictus submediterraneus</i> (Pauly, 2015)	Hal.subm	7	18	2	27	3
<i>Halictus tumulorum</i> (Linnaeus, 1758)	Hal.tum	3	4	7	14	
<i>Heriades truncorum</i> (Linnaeus, 1758)	Her.tru			3	3	
<i>Hoplitis adunca</i> (Panzer, 1798)	Hop.adu	1	1	1	3	
<i>Hoplitis claviventris</i> (Thomson, 1872)	Hop.cla	1	1		2	
<i>Hoplitis leucomelana</i> (Kirby, 1802)	Hop.leu	8	2	11	21	
<i>Hoplitis mitis</i> (Nylander, 1852)	Hop.mit			1	1	2
<i>Hylaeus angustatus</i> (Schenck, 1861)	Hyl.ang	6	3	7	16	
<i>Hylaeus brevicornis</i> Nylander, 1852	Hyl.bre	10	10	10	30	
<i>Hylaeus communis</i> Nylander, 1852	Hyl.com	1	4	1	6	
<i>Hylaeus confusus</i> Nylander, 1852	Hyl.con	1		4	5	
<i>Hylaeus difformis</i> (Eversmann, 1852)	Hyl.dif			1	1	
<i>Hylaeus dilatatus</i> (Kirby, 1802)	Hyl.dil	13	16	27	56	
<i>Hylaeus duckei</i> (Alfken, 1904)	Hyl.duc		1	4	5	3
<i>Hylaeus gibbus</i> Saunders, 1850	Hyl.gib	10	10	24	44	
<i>Hylaeus gredleri</i> Förster, 1871	Hyl.gre	1		3	4	
<i>Hylaeus hyalinatus</i> Smith, 1842	Hyl.hya		1	2	3	
<i>Hylaeus nigritus</i> (Fabricius, 1798)	Hyl.nig		2	4	6	
<i>Hylaeus punctatus</i> (Brullé, 1832)	Hyl.pun	1			1	
<i>Hylaeus variegatus</i> (Fabricius, 1798)	Hyl.var		4	1	5	V
<i>Lasioglossum albipes</i> (Fabricius, 1781)	Las.alb	1	1	2	4	
<i>Lasioglossum calceatum</i> (Scopoli, 1763)	Las.cal	15	18	9	42	
<i>Lasioglossum costulatum</i> (Kriechbaumer, 1873)	Las.cos	2			2	3
<i>Lasioglossum fulvicorne</i> (Kirby, 1802)	Las.ful		1		1	
<i>Lasioglossum glabriusculum</i> (Morawitz, 1872)	Las.gla	6	5	4	15	
<i>Lasioglossum interruptum</i> (Panzer, 1798)	Las.int	5	11	4	20	3
<i>Lasioglossum laticeps</i> (Schenck, 1868)	Las.lat	151	159	103	413	
<i>Lasioglossum lativentre</i> (Schenck, 1853)	Las.lav	1	1	2	4	V
<i>Lasioglossum leucozonium</i> (Schränk, 1781)	Las.leu			1	1	
<i>Lasioglossum lineare</i> (Schenck, 1868)	Las.lin	40	53	36	129	3
<i>Lasioglossum malachurum</i> (Kirby, 1802)	Las.mal	195	177	37	409	
<i>Lasioglossum morio</i> (Fabricius, 1793)	Las.mor	120	178	125	423	
<i>Lasioglossum pauperatum</i> (Brullé, 1832)	Las.pau	1	1		2	2
<i>Lasioglossum pauxillum</i> (Schenck, 1853)	Las.paux	48	25	21	94	
<i>Lasioglossum politum</i> (Schenck, 1853)	Las.pol	38	18	24	80	
<i>Lasioglossum punctatissimum</i> (Schenck, 1853)	Las.pun	1			1	
<i>Lasioglossum cf. pygmaeum</i>			1		1	G
<i>Lasioglossum rufitarse</i> (Zetterstedt, 1838)	Las.ruf			2	2	
<i>Lasioglossum cf. setulosum</i>		1		1	2	3
<i>Lasioglossum smeathmanellum</i> (Kirby, 1802)	Las.sme	12	17	12	41	
<i>Lasioglossum tricinctum</i> (Schenck, 1874)	Las.tri	3	5	1	9	3
<i>Lasioglossum villosulum</i> (Kirby, 1802)	Las.vil	4	3	1	8	
<i>Megachile centuncularis</i> (Linnaeus, 1758)	Meg.cen	1		2	3	V
<i>Megachile pilidens</i> Alfken, 1924	Meg.pil	2	5	2	9	3
<i>Melitta haemorrhoidalis</i> (Fabricius, 1775)	Mel.hae	1	1	1	3	
<i>Nomada bifasciata</i> Olivier, 1811	Nom.bif	2	1	4	7	
<i>Nomada fabriciana</i> (Linnaeus, 1767)	Nom.fab	2		3	5	
<i>Nomada flavoguttata</i> (Kirby, 1802)	Nom fla	3	1	11	15	
<i>Nomada fucata</i> Panzer, 1798	Nom.fuc	1	2	2	5	
<i>Nomada lathburiana</i> (Kirby, 1802)	Nom.lat	1			1	
<i>Nomada panzeri</i> Lepeletier, 1841	Nom.pan			1	1	

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<i>Nomada signata</i> Jurine, 1807	Nom.sig		1		1	
<i>Osmia aurulenta</i> (Panzer, 1799)	Osm.aur	3	1	2	6	
<i>Osmia bicolor</i> (Schränk, 1781)	Osm.bico	14	5	9	28	
<i>Osmia bicornis</i> (Linnaeus, 1758)	Osm.bic	12	9	5	26	
<i>Osmia brevicornis</i> (Fabricius, 1798)	Osm.bre			1	1	G
<i>Osmia caerulescens</i> (Linnaeus, 1758)	Osm.cae		1	1	2	
<i>Osmia cornuta</i> (Latreille, 1805)	Osm.cor			1	1	
<i>Osmia leaiana</i> (Kirby, 1802)	Osm.lea			1	1	3
<i>Panurgus dentipes</i> Latreille, 1811	Pan.den	105	43	66	214	3
<i>Pseudoanthidium nanum</i> (Mocsáry, 1879)	Pse.nan	1			1	3
<i>Sphecodes croaticus</i> Meyer, 1922	Sph.cro		1		1	2
<i>Sphecodes ephippius</i> (Linnaeus, 1767)	Sph.eph	1			1	
<i>Sphecodes ferruginatus</i> Hagens, 1882	Sph.fer	1	4		1	
<i>Systropha planidens</i> Giraud, 1861	Sys.pla	8	10	21	39	2
Total		1189	1184	1012	3385	

¹ Status of conservation concern with V – near threatened, G – threat of unknown extent, 3 – endangered, 2 – critically endangered

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Table C. 2: Effects of vineyard type on local vegetation parameters (N = 15). (G)LMMs were used with vineyard triplet as a random factor and winegrower as a random factor for number of spraying events. Different letters indicate significant differences between vineyard types ($p < 0.05$).

Variable	Vertically oriented	Terrace	Fallow	Distribution
Vegetation height [cm]	22.00 ^b ± 2.20	37.19 ^a ± 2.34	40.08 ^a ± 4.38	Gaussian
Shrub height* [cm]	0.00 ^c ± 0.00	19.44 ^b ± 5.78	119.25 ^a ± 9.69	Gaussian
Bare ground cover [%]	49.26 ^a ± 6.86	28.50 ^b ± 3.72	15.11 ^c ± 2.75	Gaussian
Vegetation cover [%]	46.80 ^b ± 5.90	63.00 ^a ± 3.45	21.69 ^c ± 4.48	Gaussian
Shrub cover [%]	0.00 ^b ± 0.00	10.22 ^b ± 3.08	63.33 ^a ± 6.06	Gaussian
Flower cover [%]	14.66 ^b ± 1.61	23.44 ^a ± 3.31	6.00 ^c ± 1.48	Gaussian
Nr. of flowering species	4.08 ^b ± 0.38	6.00 ^a ± 0.43	1.44 ^c ± 0.35	Conway-Maxwell
Nr. of spraying events	7.80 ± 1.74	6.93 ± 2.15	-	Poisson

* Square-root transformed data were used for testing

Table C. 3: Differences between vineyard types for species richness of above-ground-nesting, ground-nesting bees, and abundances of above-ground-nesting bees and ground-nesting bees. The presented estimates and p-values are obtained from post-hoc pairwise comparison of single models $Y \sim \text{Intercept} + \text{vineyard type}$ with vineyard triplet as random factor. Respective p-values are given ($p < 0.05$).

Variable	Contrast	Estimate	SE	p-Value	Distribution
Wild bee species richness	Fallow/Terrace	0.11	0.06	0.1194	Conway-Maxwell
	Fallow/Vertically oriented	0.17	0.06	0.0133	
	Terrace/Vertically oriented	0.06	0.06	0.6069	
Wild bee abundance	Fallow/Terrace	-0.05	0.14	0.9284	Negative binomial
	Fallow/Vertically oriented	-0.06	0.14	0.9097	
	Terrace/Vertically oriented	-0.01	0.14	0.9988	
Above-ground-nesting species richness	Fallow/Terrace	0.49	0.15	0.0052	Conway-Maxwell
	Fallow/Vertically oriented	0.49	0.15	0.0052	
	Terrace/Vertically oriented	-0.01	0.16	1.0000	
Above ground-nesting abundance	Fallow/Terrace	0.66	0.19	0.0034	Negative binomial
	Fallow/Vertically oriented	0.58	0.19	0.0105	
	Terrace/Vertically oriented	-0.08	0.20	0.9158	
Ground-nesting species richness	Fallow/Terrace	-0.08	0.06	0.3311	Conway-Maxwell
	Fallow/Vertically oriented	0.01	0.06	0.9873	
	Terrace/Vertically oriented	0.09	0.06	0.2613	
Ground-nesting species abundance	Fallow/Terrace	-0.19	0.15	0.4093	Negative binomial
	Fallow/Vertically oriented	-0.19	0.15	0.3966	
	Terrace/Vertically oriented	-0.01	0.14	0.9998	
Threatened wild bee species richness	Fallow/Terrace	-0.09	0.14	0.7493	Conway-Maxwell
	Fallow/Vertically oriented	0.04	0.14	0.9547	
	Terrace/Vertically oriented	0.14	0.14	0.5712	
Threatened wild bee abundance	Fallow/Terrace	0.04	0.22	0.9855	Negative binomial
	Fallow/Vertically oriented	-0.11	0.22	0.8594	
	Terrace/Vertically oriented	-0.15	0.22	0.7740	

Table C. 4: Correlation of environmental parameters with the first two RDA components related to bee species composition. Environmental variables that were significantly related to the RDA axes ($p < 0.05$, 9999 permutations) are printed in bold. Asterisks indicate significance levels ($p < 0.05=*$, $p < 0.005=**$, $p < 0.001=***$).

Variable	RDA1	RDA2	Pr (>r)
Vegetation height	-0.2538	0.9673	0.0220 *
Shrub height	-0.7126	0.7016	0.0400 *
Bare ground cover	0.0981	-0.9926	0.0540
Vegetation cover	0.9179	-0.3969	0.2230
Shrub cover	-0.4522	0.8919	0.0190 *
Flower cover	0.8900	-0.4559	0.0020 **
Nr. of flowering species	0.5625	-0.8568	0.0080 **
Soil	-0.9855	-0.1697	0.0010 ***
SNH cover	-0.9931	-0.1175	0.0010 ***
SNH distance	-0.9409	-0.2853	0.0010 ***
Forest cover	-0.9409	-0.3386	0.0220 *
Forest distance	0.9981	-0.0622	0.0010 ***
Vineyard cover	0.9658	0.2593	0.0010 ***

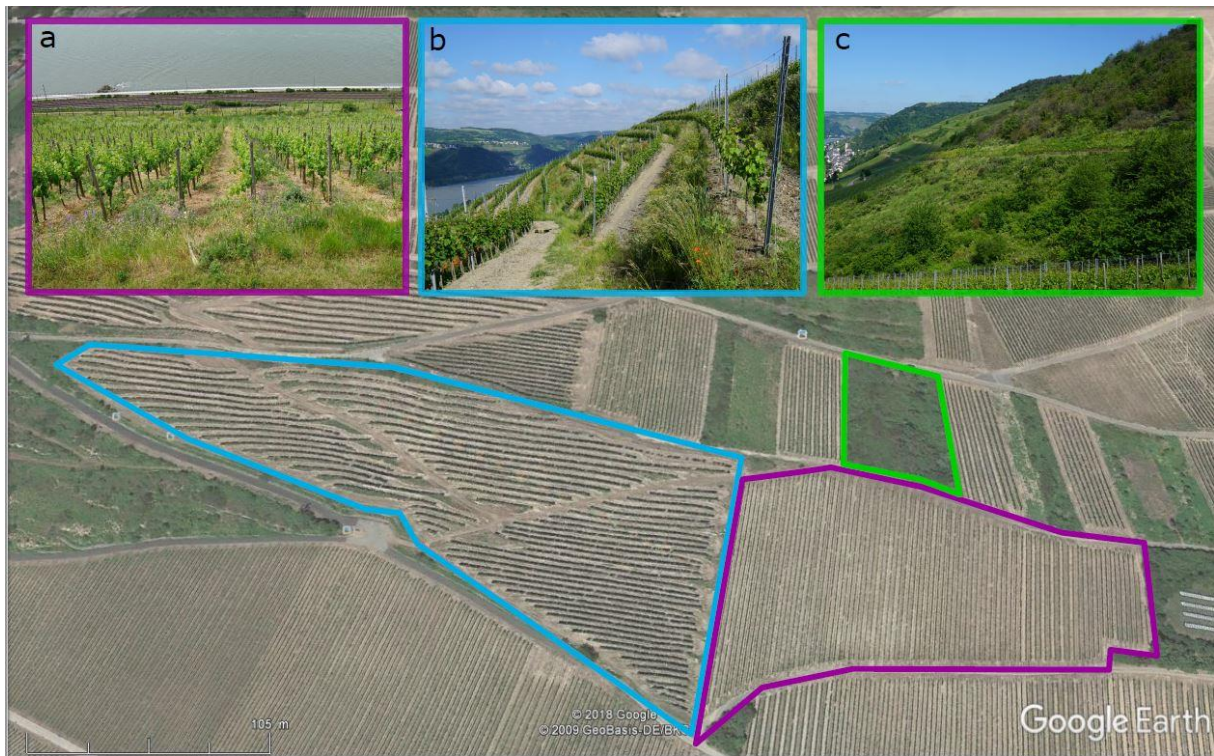


Figure C. 1: Three vineyard types were studied: terraced vineyards (a), vineyards with vertically oriented rows (b), and vineyard fallows (c). Terraced vineyard embankments were permanently covered with vegetation and managed extensively. Inter-rows of terraced vineyards were tilled. Vertically oriented vineyards usually received an alternating tillage treatment. Vineyard fallows were not managed and abandoned for at least 10 years.

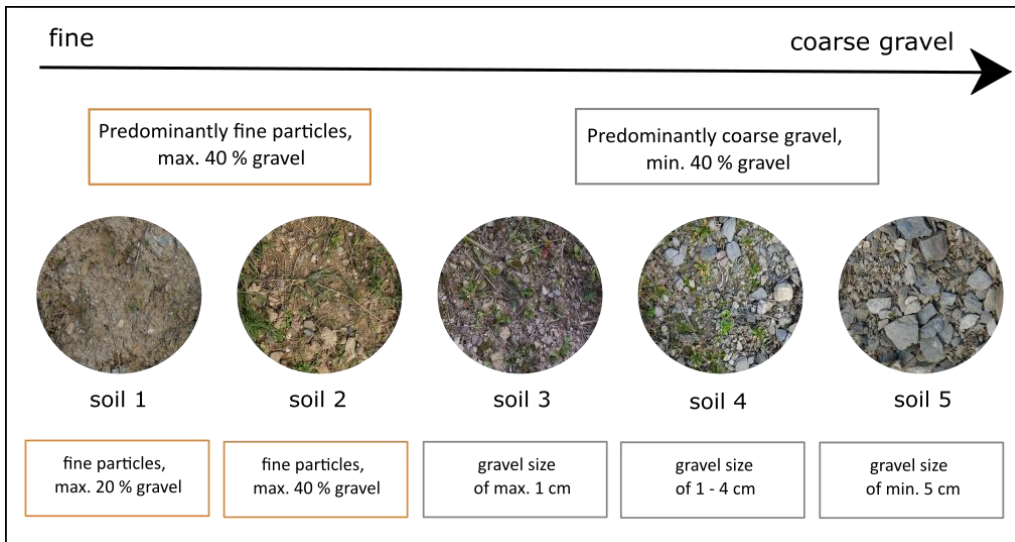


Figure C. 2: The soil was classified along a gradient from fine to coarse soil particles by visually estimating the proportion and size of fine (< 2 mm) and coarse soil particles in a rectangle of 0.4 × 0.4 m. Coarse soil particles were subdivided into three groups according to their size: max. 1 cm, 1–4 cm, and min. 5 cm

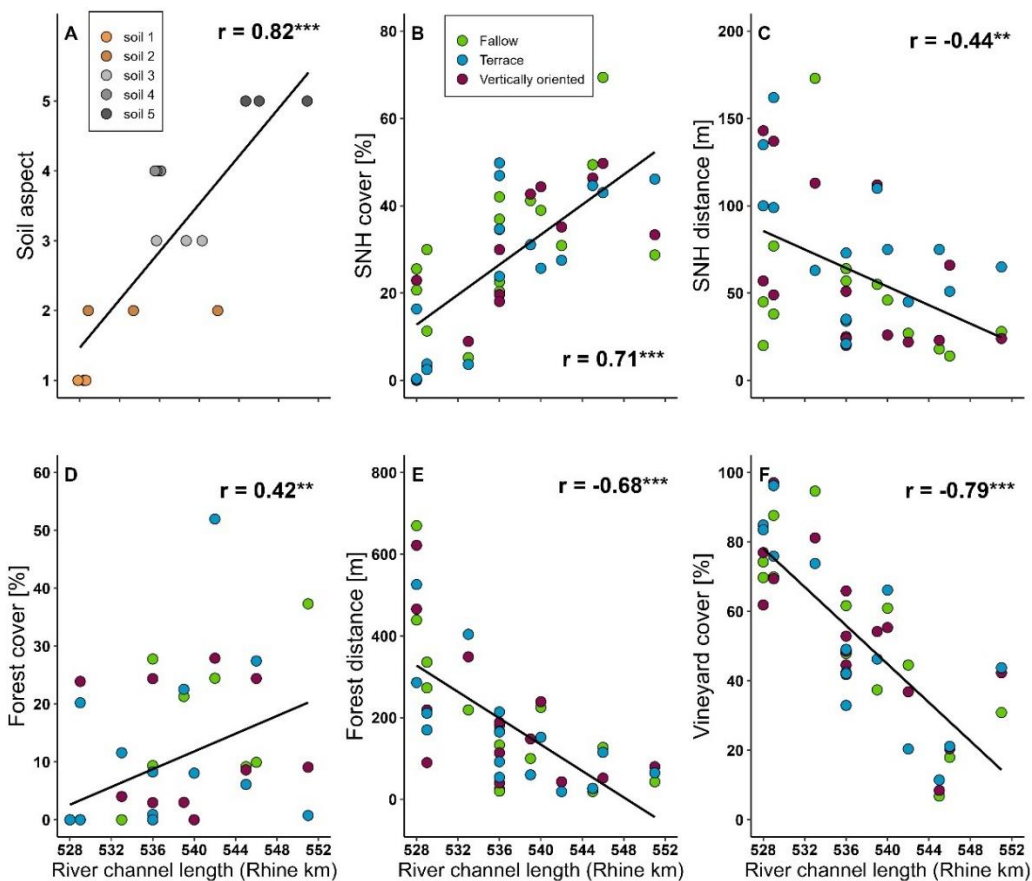


Figure C. 3: Correlation between Rhine kilometres (as a measure of river channel length) and soil aspect (A), percentage cover of SNH (B), vineyard (C), forest (D), and distance to SNH (E) and forest (F). For soil type, each data point represents one vineyard triplet. Pearson correlation coefficients (r) are given. Asterisks indicate significance levels ($p < 0.05 = *$, $p < 0.005 = **$, $p < 0.001 = ***$).

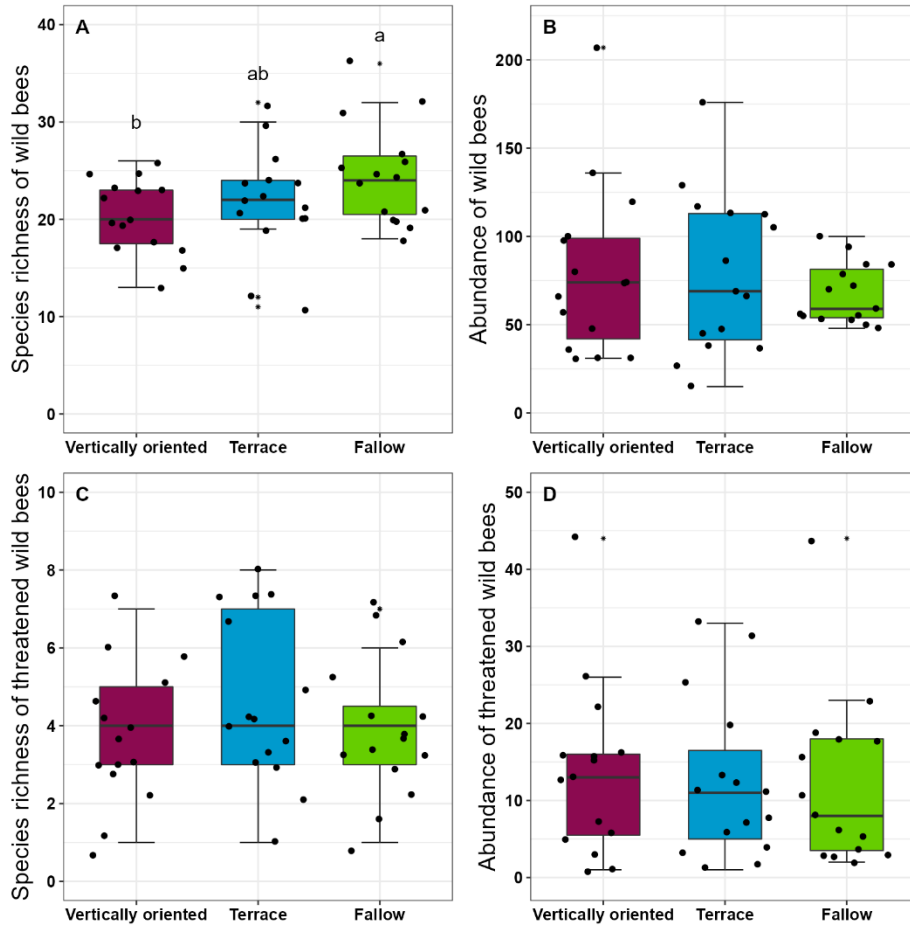


Figure C. 4: Differences between vineyard types for species richness (A) and abundance (B) of wild bees and species richness (C) and abundance (D) of threatened bees analysed using GLMMs. Each data point represents the number of species or individuals for the respective vineyard type (N = 15). Different letters indicate significant differences between vineyard types ($p < 0.05$). Respective p -values are given in Table C. 3.

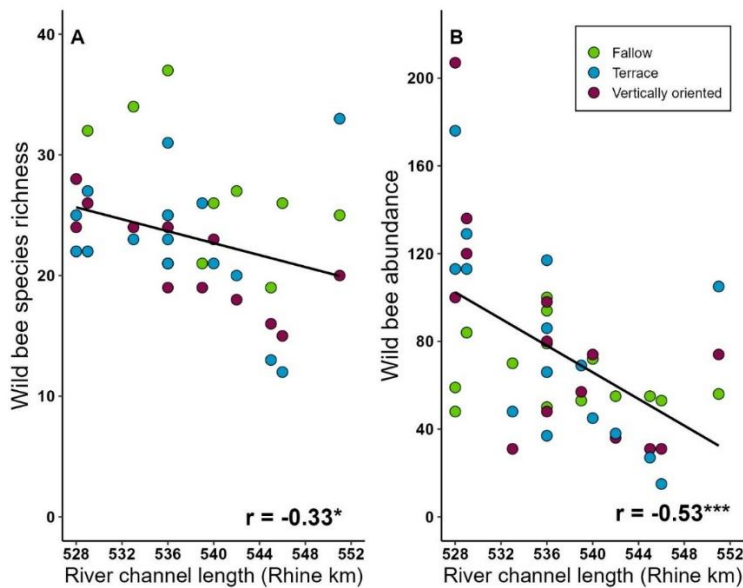


Figure C. 5: Correlation between Rhine km (as a measure of river channel length) and species richness (A) and abundance (B) of wild bees. Pearson correlation coefficients (r) are given. Asterisks indicate significance levels ($p < 0.05=*$, $p < 0.005=**$, $p < 0.001=***$).

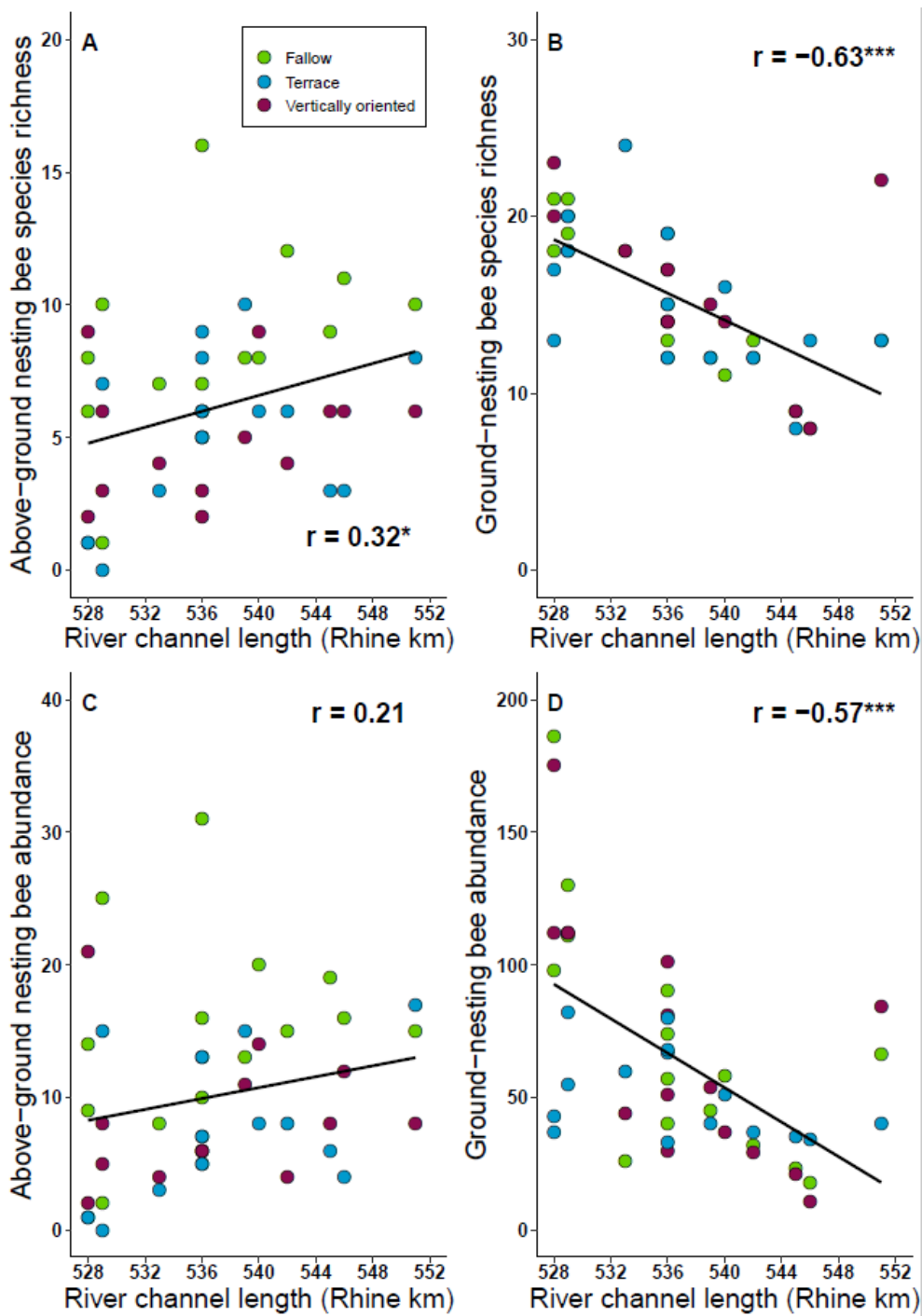


Figure C. 6: Correlation between Rhine kilometres (as a measure of river channel length) and above-ground-nesting bee species richness (A), ground-nesting bee species richness (B), and above-ground-nesting bee abundance (C), and ground-nesting bee abundance (D). Alongside the river current, the soil aspect alters from fine and loamy to coarse gravel particles, see Figure C. 2 and Figure C. 3 for details. Pearson correlation coefficients (r) are given. Asterisks indicate significance levels ($p < 0.05=*$, $p < 0.005=**$, $p < 0.001=***$).

Appendix D – Chapter 6

Table D. 1: Abundances of all adult spider species of conservation concern according to the Red List for spiders in Germany (Blick et al. 2016) for the three vineyard types sorted by family.

Family	Species	Vertically oriented	Terrace	Fallow	Total	Status
Dictynidae	<i>Brigittea latens</i> (Fabricius, 1775)		1	2	3	threat of unknown extend
Gnaphosidae	<i>Drassyllus villicus</i> (Thorell, 1875)	7	21	57	85	near threatened
	<i>Phaeocedus braccatus</i> (L. Koch, 1866)		2	1	3	endangered
	<i>Zelotes aeneus</i> (Simon, 1878)	17	9	5	31	near threatened
	<i>Zelotes exiguus</i> (Müller & Schenkel, 1895)	45	40	14	99	threat of unknown extend
	<i>Zelotes gallicus</i> Simon, 1914			1	1	critically endangered
<i>Zelotes puritanus</i> Chamberlin, 1922	5	6	9	20	critically endangered	
Hahniidae	<i>Hahnia petrobia</i> Simon, 1875	9	5	5	19	critically endangered
	<i>Iberina candida</i> (Simon, 1875)	1	3		4	endangered
Linyphiidae	<i>Acartauchenius scurrilis</i> (O. Pickard-Cambridge, 1873)	1	1		2	threat of unknown extend
	<i>Centromerus capucinus</i> (Simon, 1884)			1	1	threat of unknown extend
	<i>Ipa keyserlingi</i> (Ausserer, 1867)		1	2	3	endangered
Lycosidae	<i>Pardosa bifasciata</i> (C. L. Koch, 1834)	2	6	12	20	near threatened
	<i>Trochosa robusta</i> (Simon, 1876)	10	8	4	22	near threatened
Salticidae	<i>Chalcoscirtus infimus</i> (Simon, 1868)	14	25	7	46	endangered
	<i>Heliophanus auratus</i> C. L. Koch, 1835	1		1	2	near threatened
	<i>Heliophanus tribulosus</i> Simon, 1868	1		2	3	endangered
		113	128	123	364	

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Blick, T.; Finch, O.-D.; Harms, K. H.; Kiechle, J.; Kielhorn, K.-H.; Kreuels, M. et al. (2016): Rote Liste und Gesamtartenliste der Spinnen (Arachnida: Araneae) Deutschlands. 3. Fassung. Naturschutz und biologische Vielfalt. 70.

Table D. 2: Abundances of all collected spiders in vertically oriented vineyards, terraced vineyards and vineyard fallows sorted by family. Nomenclature follows World Spider Catalog Version 22.0. Entries without code were not included in analyses of species richness or community composition because they represent either immature spiders or indeterminable (due to deformed or destroyed genitalia) spiders.

Family	Species	Code	LSID	Vertically oriented	Terrace	Fallow	Total
Agelenidae	<i>Coelotes terrestris</i> (Wider, 1834)	Coe.ter	urn:lsid:nmbe.ch:spidersp:022890		1		1
	<i>Eratigena agrestis</i> (Walckenaer, 1802)	Era.agr	urn:lsid:nmbe.ch:spidersp:021188	15	12		27
	<i>Eratigena picta</i> (Simon, 1870)	Era.pic	urn:lsid:nmbe.ch:spidersp:021276		2		2
	<i>Histopona torpida</i> (C. L. Koch, 1837)	His.tor	urn:lsid:nmbe.ch:spidersp:020976	1	1	5	7
	<i>Tegenaria domestica</i> (Clerck, 1757)	Teg.dom	urn:lsid:nmbe.ch:spidersp:021218		1	1	2
	immature			2	4	3	8
Amaurobiidae	immature					2	2
Araneidae	<i>Larinioides patagiatus</i> (Clerck, 1757)	Lar.pat	urn:lsid:nmbe.ch:spidersp:016290	2	2		4
	<i>Mangora acalypha</i> (Walckenaer, 1802)	Man.aca	urn:lsid:nmbe.ch:spidersp:016308			1	1
	immature			1	6	2	9
Cheiracanthiidae	immature				1	2	3
Clubionidae	<i>Clubiona terrestris</i> Westring, 1851	Clu.ter	urn:lsid:nmbe.ch:spidersp:024795			1	1
	immature				1	5	6
Dictynidae	<i>Argenna subnigra</i> (O. Pickard-Cambridge, 1861)	Arg.sub	urn:lsid:nmbe.ch:spidersp:022086	9	3	2	14
	<i>Brigittea latens</i> (Fabricius, 1775)	Bri.lat	urn:lsid:nmbe.ch:spidersp:022296		1	2	3
	immature			1	1		2
Dysderidae	<i>Dysdera crocata</i> C. L. Koch, 1838	Dys.cro	urn:lsid:nmbe.ch:spidersp:004397	4	5	2	11
	<i>Dysdera erythrina</i> (Walckenaer, 1802)	Dys.ery	urn:lsid:nmbe.ch:spidersp:004414	3	2	3	8
	<i>Harpactea hombergi</i> (Scopoli, 1763)	Har.hom	urn:lsid:nmbe.ch:spidersp:004656			1	1
	<i>Harpactea rubicunda</i> (C. L. Koch, 1838)	Har.rub	urn:lsid:nmbe.ch:spidersp:004709	1		1	2
	immature			10	16	8	34
Gnaphosidae	<i>Callilepis nocturna</i> (Linnaeus, 1758)	Cal.noc	urn:lsid:nmbe.ch:spidersp:026717	38	20	9	67
	<i>Drassodes lapidosus</i> (Walckenaer, 1802)	Dra.lap	urn:lsid:nmbe.ch:spidersp:026926	34	45	13	92
	<i>Drassodes pubescens</i> (Thorell, 1856)	Dra.pub	urn:lsid:nmbe.ch:spidersp:026977		2		2
	<i>Drassyllus praefficus</i> (L. Koch, 1866)	Dra.pra	urn:lsid:nmbe.ch:spidersp:027082	35	28	28	91

	<i>Drassyllus pumilus</i> (C. L. Koch, 1839)	Dra.pum	urn:lsid:nmbe.ch:spidersp:027086	33	46	7	86
	<i>Drassyllus pusillus</i> (C. L. Koch, 1833)	Dra.pus	urn:lsid:nmbe.ch:spidersp:027087	7	2	1	10
	<i>Drassyllus villicus</i> (Thorell, 1875)	Dra.vil	urn:lsid:nmbe.ch:spidersp:027104	7	21	57	85
	<i>Haplodrassus signifer</i> (C. L. Koch, 1839)	Hap.sig	urn:lsid:nmbe.ch:spidersp:027360	54	37	9	100
	<i>Haplodrassus silvestris</i> (Blackwall, 1833)	Hap.sil	urn:lsid:nmbe.ch:spidersp:027361			1	1
	<i>Haplodrassus umbratilis</i> (L. Koch, 1866)	Hap.umb	urn:lsid:nmbe.ch:spidersp:027367			1	1
	<i>Micaria micans</i> (Sundevall, 1831)	Mic.pul	urn:lsid:nmbe.ch:spidersp:051639		1		1
	<i>Phaeoedus braccatus</i> (L. Koch, 1866)	Pha.bra	urn:lsid:nmbe.ch:spidersp:027713		2	1	3
	<i>Trachyzelotes pedestris</i> (C. L. Koch, 1837)	Tra.ped	urn:lsid:nmbe.ch:spidersp:028035	15	15	67	97
	<i>Zelotes aeneus</i> (Simon, 1878)	Zel.aen	urn:lsid:nmbe.ch:spidersp:028103	17	9	5	31
	<i>Zelotes exiguus</i> (Müller & Schenkel, 1895)	Zel.exi	urn:lsid:nmbe.ch:spidersp:028196	45	40	14	99
	<i>Zelotes gallicus</i> Simon, 1914	Zel.gal	urn:lsid:nmbe.ch:spidersp:028218			1	1
	<i>Zelotes longipes</i> (L. Koch, 1866)	Zel.lon	urn:lsid:nmbe.ch:spidersp:028285			1	1
	<i>Zelotes petrensis</i> (C. L. Koch, 1839)	Zel.pet	urn:lsid:nmbe.ch:spidersp:028338	21	48	24	93
	<i>Zelotes puritanus</i> Chamberlin, 1922	Zel.pur	urn:lsid:nmbe.ch:spidersp:028356	5	6	9	20
	<i>Zelotes subterraneus</i> (C. L. Koch, 1833)	Zel.sub	urn:lsid:nmbe.ch:spidersp:028403		2	4	6
	immature			67	102	66	235
	<i>Drassodes</i> cf. <i>lapidosus</i>			1			1
	<i>Haplodrassus</i> cf. <i>signifer</i>			1			1
	<i>Zelotes</i> sp.				1		1
Hahniidae	<i>Cicurina cicur</i> (Fabricius, 1793)	Cic.cic	urn:lsid:nmbe.ch:spidersp:022133		1	1	2
	<i>Hahnia nava</i> (Blackwall, 1841)	Hah.nav	urn:lsid:nmbe.ch:spidersp:021946	7	4	6	17
	<i>Hahnia petrobia</i> Simon, 1875	Hah.pet	urn:lsid:nmbe.ch:spidersp:021954	9	5	5	19
	<i>Hahnia pusilla</i> C. L. Koch, 1841	Hah.pus	urn:lsid:nmbe.ch:spidersp:021957	1	2		3
	<i>Iberina candida</i> (Simon, 1875)	Ibe.can	urn:lsid:nmbe.ch:spidersp:021900	1	3		4
Linyphiidae	<i>Acartauchenius scurrilis</i> (O. Pickard-Cambridge, 1873)	Aca.scu	urn:lsid:nmbe.ch:spidersp:009331	1	1		2
	<i>Agyneta rurestris</i> (C. L. Koch, 1836)	Agy.rur	urn:lsid:nmbe.ch:spidersp:011711	120	54		174
	<i>Bathyphantes parvulus</i> (Westring, 1851)	Bat.par	urn:lsid:nmbe.ch:spidersp:009588			1	1
	<i>Centromerus capucinus</i> (Simon, 1884)	Cen.cap	urn:lsid:nmbe.ch:spidersp:009720			1	1
	<i>Diplocephalus cristatus</i> (Blackwall, 1833)	Dip.cri	urn:lsid:nmbe.ch:spidersp:010052	3	1		4

	<i>Diplocephalus picinus</i> (Blackwall, 1841)	Dip.pic	urn:lsid:nmbe.ch:spidersp:010071			7	7
	<i>Diplostyla concolor</i> (Wider, 1834)	Dip.con	urn:lsid:nmbe.ch:spidersp:010092	6			6
	<i>Erigone atra</i> Blackwall, 1833	Eri.atr	urn:lsid:nmbe.ch:spidersp:010400	5	1		6
	<i>Erigone dentipalpis</i> (Wider, 1834)	Eri.den	urn:lsid:nmbe.ch:spidersp:010424	21	3	1	25
	<i>Ipa keyserlingi</i> (Ausserer, 1867)	Ipa.key	urn:lsid:nmbe.ch:spidersp:011198		1	2	3
	<i>Mermessus trilobatus</i> (Emerton, 1882)	Mer.tri	urn:lsid:nmbe.ch:spidersp:010369			1	1
	<i>Micrargus herbigradus</i> (Blackwall, 1854)	Mic.her	urn:lsid:nmbe.ch:spidersp:011784			7	7
	<i>Micrargus subaequalis</i> (Westring, 1851)	Mic.sub	urn:lsid:nmbe.ch:spidersp:011790		2		2
	<i>Palliduphantes pallidus</i> (O. Pickard-Cambridge, 1871)	Pal.pal	urn:lsid:nmbe.ch:spidersp:011270		1	1	2
	<i>Pelecopsis elongata</i> (Wider, 1834)	Pel.elo	urn:lsid:nmbe.ch:spidersp:012256		1		1
	<i>Porrhomma errans</i> (Blackwall, 1841)	Por.err	urn:lsid:nmbe.ch:spidersp:012409			1	1
	<i>Stemonyphantes lineatus</i> (Linnaeus, 1758)	Ste.lin	urn:lsid:nmbe.ch:spidersp:012760			1	1
	<i>Tenuiphantes flavipes</i> (Blackwall, 1854)	Ten fla	urn:lsid:nmbe.ch:spidersp:012874			1	1
	<i>Tenuiphantes tenuis</i> (Blackwall, 1852)	Ten.ten	urn:lsid:nmbe.ch:spidersp:012897	6	1	5	12
	immature			12	7	5	24
Liocranidae	<i>Agroeca cuprea</i> Menge, 1873	Agr.cup	urn:lsid:nmbe.ch:spidersp:024146	1	1	1	3
	<i>Apostenus fuscus</i> Westring, 1851	Apo.fus	urn:lsid:nmbe.ch:spidersp:024177			2	2
	<i>Scotina celans</i> (Blackwall, 1841)	Sco.cel	urn:lsid:nmbe.ch:spidersp:024394			1	1
	immature				1	1	2
Lycosidae	<i>Alopecosa farinosa</i> (Herman, 1879)	Alo.far	urn:lsid:nmbe.ch:spidersp:048749	4	4	5	13
	<i>Alopecosa pulverulenta</i> (Clerck, 1757)	Alo.pul	urn:lsid:nmbe.ch:spidersp:017479	4		2	6
	<i>Aulonia albimana</i> (Walckenaer, 1805)	Aul.alb	urn:lsid:nmbe.ch:spidersp:017713	124	197	295	616
	<i>Pardosa agrestis</i> (Westring, 1861)	Par.agr	urn:lsid:nmbe.ch:spidersp:018501	17	4		21
	<i>Pardosa alacris</i> (C. L. Koch, 1833)	Par.ala	urn:lsid:nmbe.ch:spidersp:018506	1	11	63	75
	<i>Pardosa bifasciata</i> (C. L. Koch, 1834)	Par.bif	urn:lsid:nmbe.ch:spidersp:018555	2	6	12	20
	<i>Pardosa hortensis</i> (Thorell, 1872)	Par.hor	urn:lsid:nmbe.ch:spidersp:018684	101	43	33	177
	<i>Pardosa</i> cf. <i>lugubris</i> s. str. (WALCKENAER, 1802)					1	1
	<i>Pardosa lugubris</i> s. str.		urn:lsid:nmbe.ch:spidersp:018747		2	4	6
	<i>Pardosa palustris</i> (Linnaeus, 1758)	Par.pal	urn:lsid:nmbe.ch:spidersp:018840	9		2	11
	<i>Pardosa prativaga</i> (L. Koch, 1870)	Par.pra	urn:lsid:nmbe.ch:spidersp:018864	6	1	1	8

	<i>Pardosa pullata</i> (Clerck, 1757)	Par.pul	urn:lsid:nmbe.ch:spidersp:018881	6	1		7
	<i>Pardosa saltans</i> Töpfer-Hofmann, 2000	Par.sal	urn:lsid:nmbe.ch:spidersp:018902	6	4	54	64
	<i>Trochosa robusta</i> (Simon, 1876)	Tro.rob	urn:lsid:nmbe.ch:spidersp:019345	10	8	4	22
	<i>Xerolycosa miniata</i> (C. L. Koch, 1834)	Xer.min	urn:lsid:nmbe.ch:spidersp:019412	7	1	1	9
	<i>Xerolycosa nemoralis</i> (Westring, 1861)	Xer.nem	urn:lsid:nmbe.ch:spidersp:019413	9			9
	immature			504	225	214	943
	<i>Pardosa cf. agrestis</i>				1		1
	<i>Pardosa alacris/saltans</i> ♀			5	3	31	39
Mimetidae	<i>Ero aphana</i> (Walckenaer, 1802)	Ero.aph	urn:lsid:nmbe.ch:spidersp:005666			1	1
Miturgidae	<i>Zora spinimana</i> (Sundevall, 1833)	Zor.spi	urn:lsid:nmbe.ch:spidersp:028562			4	4
	immature					1	1
Philodromidae	<i>Philodromus aureolus</i> (Clerck, 1757)	Phi.aur	urn:lsid:nmbe.ch:spidersp:029754		1		1
	<i>Philodromus cespitum</i> (Walckenaer, 1802)	Phi.ces	urn:lsid:nmbe.ch:spidersp:029784	1			1
	<i>Philodromus dispar</i> Walckenaer, 1826	Phi.dis	urn:lsid:nmbe.ch:spidersp:029805			1	1
	immature			1	1		2
Phrurolithidae	<i>Phrurolithus festivus</i> (C. L. Koch, 1835)	Phr.fes	urn:lsid:nmbe.ch:spidersp:024312	13	5	8	26
	<i>Phrurolithus minimus</i> C. L. Koch, 1839	Phr.min	urn:lsid:nmbe.ch:spidersp:024329	25	26	16	67
	immature			5	1	5	11
	<i>Phrurolithus sp.</i>					1	1
Pisauridae	<i>Pisaura mirabilis</i> (Clerck, 1757)	Pis.mir	urn:lsid:nmbe.ch:spidersp:019759		3	4	7
Salticidae	<i>Aelurillus v-insignitus</i> (Clerck, 1757)	Ael.v-i	urn:lsid:nmbe.ch:spidersp:032215			1	1
	<i>Attulus pubescens</i> (Fabricius, 1775)	Att.pub	urn:lsid:nmbe.ch:spidersp:036261		1		1
	<i>Ballus chalybeius</i> (Walckenaer, 1802)	Bal.cha	urn:lsid:nmbe.ch:spidersp:032403	2	1		3
	<i>Chalcoscirtus infimus</i> (Simon, 1868)	Cha.inf	urn:lsid:nmbe.ch:spidersp:032664	14	25	7	46
	<i>Euophrys frontalis</i> (Walckenaer, 1802)	Euo.fro	urn:lsid:nmbe.ch:spidersp:033272		4	2	6
	<i>Evarcha arcuata</i> (Clerck, 1757)	Eva.arc	urn:lsid:nmbe.ch:spidersp:033381			1	1
	<i>Evarcha falcata</i> (Clerck, 1757)	Eva.fal	urn:lsid:nmbe.ch:spidersp:033396			1	1
	<i>Heliophanus auratus</i> C. L. Koch, 1835	Hel.aur	urn:lsid:nmbe.ch:spidersp:033753	1		1	2
	<i>Heliophanus cupreus</i> (Walckenaer, 1802)	Hel.cup	urn:lsid:nmbe.ch:spidersp:033774	1		2	3
	<i>Heliophanus tribulosus</i> Simon, 1868	Hel.tri	urn:lsid:nmbe.ch:spidersp:033862	1		2	3

	<i>Myrmarachne formicaria</i> (De Geer, 1778)	Myr.for	urn:lsid:nmbe.ch:spidersp:034782			1	1
	<i>Pellenes tripunctatus</i> (Walckenaer, 1802)	Pel.tri	urn:lsid:nmbe.ch:spidersp:035317			1	1
	<i>Phlegra fasciata</i> (Hahn, 1826)	Phl.fas	urn:lsid:nmbe.ch:spidersp:035574	1	1		2
	<i>Salticus scenicus</i> (Clerck, 1757)	Sal.sce	urn:lsid:nmbe.ch:spidersp:036032	1	1		2
	<i>Sibianor aurocinctus</i> (Ohlert, 1865)	Sib.aur	urn:lsid:nmbe.ch:spidersp:032519		3	4	7
	<i>Talavera aequipes</i> (O. Pickard-Cambridge, 1871)	Tal.aeq	urn:lsid:nmbe.ch:spidersp:036445	1	3	1	5
	<i>Talavera aperta</i> (Miller, 1971)	Tal.ape	urn:lsid:nmbe.ch:spidersp:038310	2	1		3
	<i>Talavera inopinata</i> Wunderlich, 1993	Tal.ino	urn:lsid:nmbe.ch:spidersp:036448	1	4	3	8
	immature			1	4	8	13
Scytodidae	<i>Scytodes thoracica</i> (Latreille, 1802)	Scy.tho	urn:lsid:nmbe.ch:spidersp:002900			1	1
Segestriidae	<i>Segestria bavarica</i> C. L. Koch, 1843	Seg.bav	urn:lsid:nmbe.ch:spidersp:004302	1			1
Tetragnathidae	<i>Pachygnatha degeeri</i> Sundevall, 1830	Pac.deg	urn:lsid:nmbe.ch:spidersp:014028	1			1
Theridiidae	<i>Anelosimus vittatus</i> (C. L. Koch, 1836)	Ane.vit	urn:lsid:nmbe.ch:spidersp:006962		1		1
	<i>Asagena phalerata</i> (Panzer, 1801)	Asa.pha	urn:lsid:nmbe.ch:spidersp:008101	11	8	1	20
	<i>Enoplognatha thoracica</i> (Hahn, 1833)	Eno.tho	urn:lsid:nmbe.ch:spidersp:007595	4	12	12	28
	<i>Episinus truncatus</i> Latreille, 1809	Epi.tru	urn:lsid:nmbe.ch:spidersp:007677		3	2	5
	<i>Euryopsis flavomaculata</i> (C. L. Koch, 1836)	Eur fla	urn:lsid:nmbe.ch:spidersp:007704	1			1
	<i>Neottiura bimaculata</i> (Linnaeus, 1767)	Neo.bim	urn:lsid:nmbe.ch:spidersp:007852			1	1
	<i>Robertus lividus</i> (Blackwall, 1836)	Rob.liv	urn:lsid:nmbe.ch:spidersp:007977		1	4	5
	immature			2	2	1	5
Thomisidae	<i>Ozyptila atomaria</i> (Panzer, 1801)	Ozy.ato	urn:lsid:nmbe.ch:spidersp:030828			1	1
	<i>Ozyptila claveata</i> (Walckenaer, 1837)	Ozy.cla	urn:lsid:nmbe.ch:spidersp:030838		5	2	7
	<i>Ozyptila praticola</i> (C. L. Koch, 1837)	Ozy.pra	urn:lsid:nmbe.ch:spidersp:030893			30	30
	<i>Ozyptila simplex</i> (O. Pickard-Cambridge, 1862)	Ozy.sim	urn:lsid:nmbe.ch:spidersp:030904	5		4	9
	<i>Xysticus cristatus</i> (Clerck, 1757)	Xys.cri	urn:lsid:nmbe.ch:spidersp:031858	4	1	1	6
	<i>Xysticus kochi</i> Thorell, 1872	Xys.koc	urn:lsid:nmbe.ch:spidersp:031951	11	5	2	18
	immature			9	5	2	16
	<i>Ozyptila cf. claveata</i>				1		1
	<i>Ozyptila cf. praticola</i>					1	1
Titanoecidae	<i>Titanoeca quadriguttata</i> (Hahn, 1833)	Tit.qua	urn:lsid:nmbe.ch:spidersp:023207	91	120	13	224

	immature			5	8	4	17
Zodariidae	<i>Zodarion italicum</i> (Canestrini, 1868)	Zod.ita	urn:lsid:nmbe.ch:spidersp:026078	335	508	219	1062
	<i>Zodarion rubidum</i> Simon, 1914	Zod.rub	urn:lsid:nmbe.ch:spidersp:026117	12	7	5	24
	immature			37	56	29	121
	<i>Zodarion cf. italicum</i>				1	2	3
Total				2037	1916	1545	5496

References:

World Spider Catalog (2020): World Spider Catalog. Version 21.5: Natural History Museum Bern. Available online at <https://wsc.nmbe.ch/>.

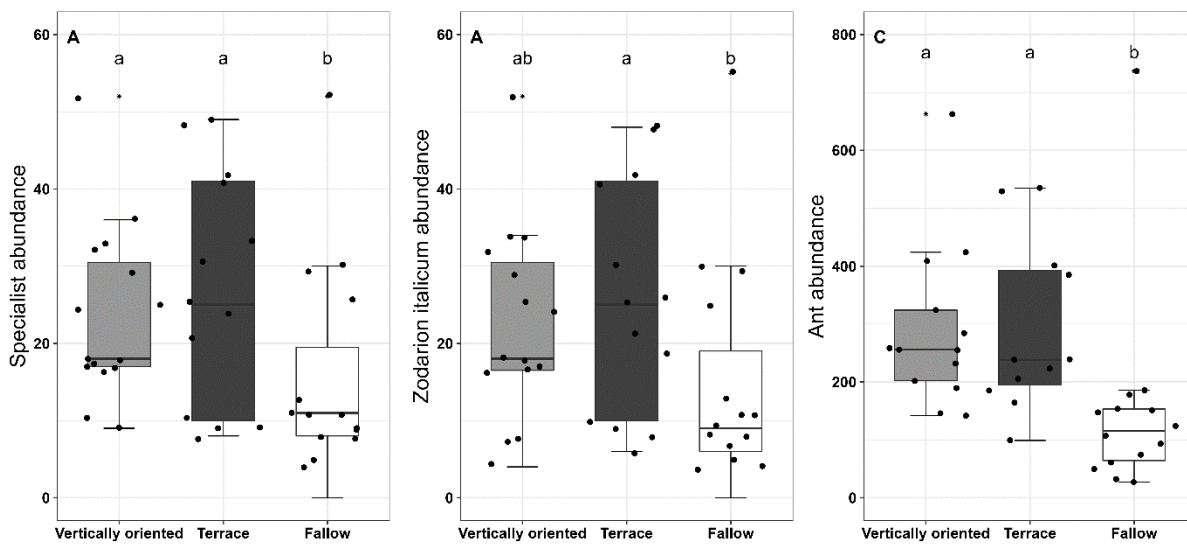


Figure D. 1: Boxplots show differences in the abundance of specialists (A), *Z. italicum* (B) and ant individuals (C) between vineyard types analysed using GLMMs. Each data point represents mean values per site (N = 15). Different letters indicate significant differences between vineyard types ($p < 0.05$).

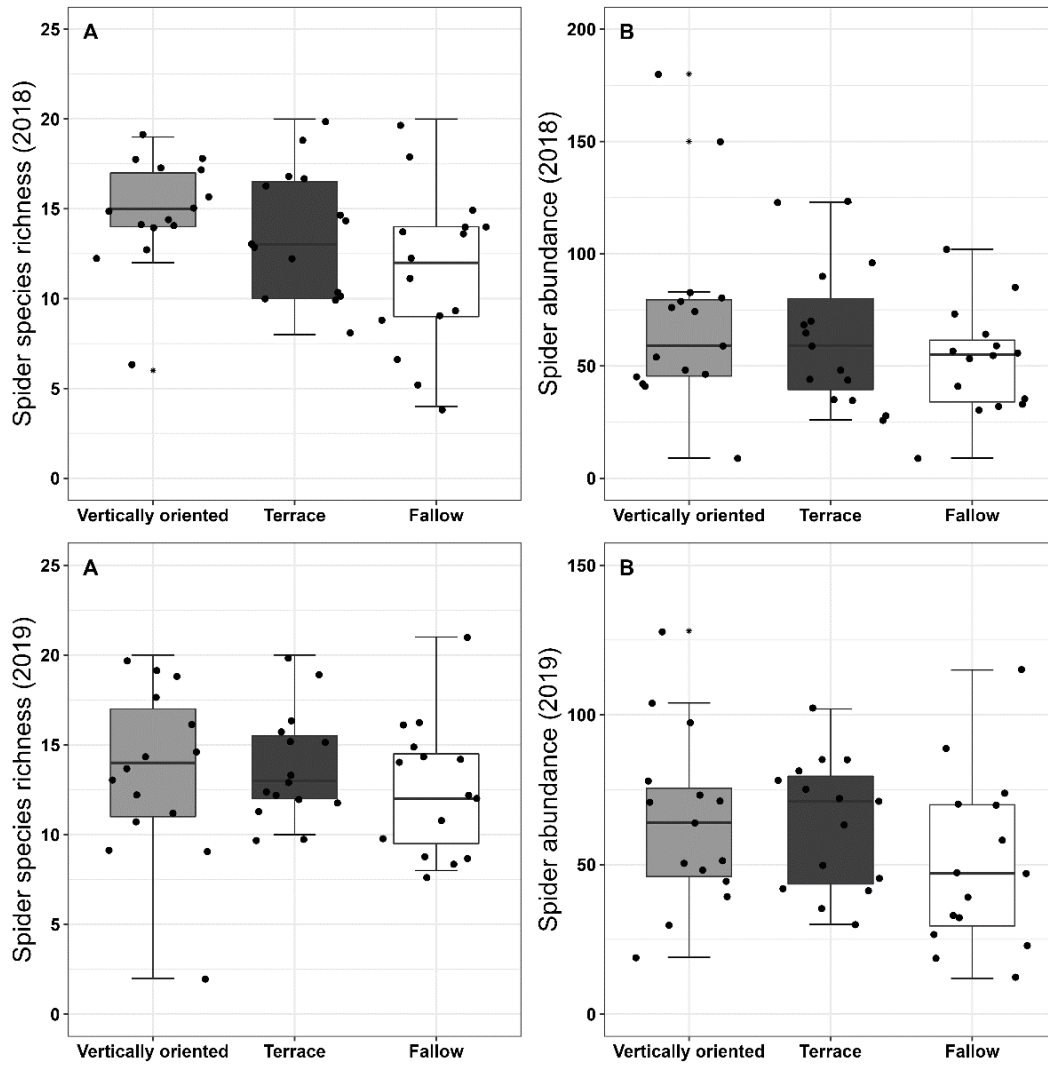


Figure D. 2: Boxplots show differences in spider species richness and abundance between vineyard types for 2018 (A, B) and 2019 (C, D) analysed using GLMMs. Each data point represents mean values per site (N = 15).

Appendix E – Chapter 7

Table E. 1: List of plant species of commercial and regional mixture sown in 2018.

Species	Seed proportion [% by weight]		Production area of seeds	
	Commercial mixture (RSM 7.22)	Regional mixture	Country	Region
<i>Achillea millefolium</i>	0.20	1.00	Germany	Germany, West German low mountain region
<i>Agrimonia eupatoria</i>		2.00		Germany, West German low mountain region
<i>Agrostis capillaris</i>		2.00		Germany, West German low mountain region
<i>Anthemis tinctoria</i>		0.50		Germany, West German low mountain region
<i>Anthoxanthum odoratum</i>		3.00		Germany, West German low mountain region
<i>Anthyllis vulneraria</i>	0.20		Germany	
<i>Briza media</i>		2.00		Germany, West German low mountain region
<i>Bromus erectus</i>		5.00		Germany, West German low mountain region
<i>Campanula rapunculus</i>		0.10		Germany, West German low mountain region
<i>Centaurea jacea</i>	0.10	1.00	Germany	Germany, West German low mountain region
<i>Centaurea scabiosa</i>	0.10	0.50	Germany	Germany, West German low mountain region
<i>Clinopodium vulgare</i>		0.30		Germany, West German low mountain region
<i>Cynosurus cristatus</i>		3.00		Germany, West German low mountain region
<i>Daucus carota</i>		1.00		Germany, West German low mountain region
<i>Dianthus carthusianorum*</i>	0.10	0.50	Germany	Germany, West German low mountain region
<i>Echium vulgare</i>		1.50		Germany, West German low mountain region
<i>Festuca guestfalica</i>		25.00		Germany, West German low mountain region
<i>Festuca rubra</i>		20.00		Germany, West German low mountain region
<i>Festuca rubra commutata</i> MISSION**	15.00		Denmark	
<i>Festuca rubra rubra</i> MAXIMA 1**	15.00		Denmark	
<i>Festuca rubra trichophylla</i> BORLUNA**	10.00		Benelux countries	
<i>Festuca trachyphylla</i> BORNITO**	41.90		Germany	
<i>Galium album</i>		1.50		Germany, West German low mountain region
<i>Galium mollugo</i>	0.10		Germany	
<i>Galium verum</i>	0.10	0.40	Germany	Germany, West German low mountain region
<i>Hypericum perforatum</i>		0.50		Germany, West German low mountain region
<i>Knautia arvensis</i>		0.50		Germany, West German low mountain region
<i>Leontodon ssp.</i>			Germany	
	0.10			
<i>Leucanthemum ircutianum</i>		1.50		Germany, West German low mountain region
<i>Leucanthemum vulgare</i>	0.20		Germany	
<i>Linaria vulgaris</i>		0.20		Germany, West German low mountain region

<i>Lolium perenne</i> FANCY**	15.00		Poland	
<i>Lotus corniculatus</i>	0.20	1.50	Germany	Germany, West German low mountain region
<i>Malva moschata</i>		2.00		Germany, West German low mountain region
<i>Medicago lupulina</i>	0.20	1.50	Germany	Germany, West German low mountain region
<i>Onobrychis viciifolia</i>	0.80		Germany	
<i>Origanum vulgare</i>		0.30		Germany, West German low mountain region
<i>Picris hieracioides</i>		0.50		Germany, West German low mountain region
<i>Pimpinella saxifraga</i>	0.10	0.40	Germany	Germany, West German low mountain region
<i>Plantago lanceolata</i>	0.10	1.60	Germany	Germany, West German low mountain region
<i>Poa angustifolia</i>		5.00		Germany, West German low mountain region
<i>Poa compressa</i>		5.00		Germany, West German low mountain region
<i>Prunella vulgaris</i>		0.50		Germany, West German low mountain region
<i>Rhinanthus minor</i>		0.50		Germany, West German low mountain region
<i>Salvia pratensis</i> *	0.20	2.00	Germany	Germany, West German low mountain region
<i>Sanguisorba minor</i>	0.10	0.50	Germany	Germany, West German low mountain region
<i>Saponaria officinalis</i>		1.00		Germany, West German low mountain region
<i>Silene vulgaris</i>		2.00		Germany, West German low mountain region
<i>Thymus pulegioides</i>		0.20		Germany, West German low mountain region

* near threatened according to the Red List for plants (ferns and flowering plants) in Germany (Metzing et al 2018)

** cultivar species

References:

Metzing, D.; Garve, E.; Matzke-Hajek, G.; Adler, J.; Bleeker, W.; Breunig, T. et al. (2018): Rote Liste und Gesamtartenliste der Farn- und Blütenpflanzen (Tracheophyta) Deutschlands. Hg. v. Landwirtschaftsverlag. Naturschutz und Biologische Vielfalt 70. Münster.

Table E. 2: Effects of seeding technique on local vegetation parameters (N = 30) analysed using LMMs. The presented estimates, standard errors (SE) and *p*-values are obtained from the model $Y \sim \text{Intercept} + \text{seeding technique} + \text{vineyard site/embankment/paired plot}$ as random factor. *p*-Values below a threshold of $\alpha < 0.05$ are printed in bold.

	Year	Hydro-seeding	Manual seeding	Estimate ± SE	<i>p</i>
Bare ground cover [%]	2018	57.83 ± 4.39	61.83 ± 4.55	4.00 ± 5.08	0.4310
	2019	39.83 ± 2.37	44.33 ± 2.29	4.50 ± 3.65	0.2170
	2020	23.58 ± 1.85	32.33 ± 2.43	8.75 ± 3.51	0.0127
Herb cover [%]	2018	76.83 ± 3.59	69.50 ± 4.53	-7.33 ± 2.98	0.0139
	2019	75.33 ± 3.14	70.83 ± 3.82	-4.50 ± 4.52	0.3190
	2020	82.00 ± 2.50	80.00 ± 2.73	-1.83 ± 3.20	0.5660
Grass cover [%]	2018	23.17 ± 3.59	30.50 ± 4.53	7.33 ± 2.98	0.0139
	2019	23.33 ± 3.05	29.17 ± 3.83	5.83 ± 4.47	0.1935
	2020	18.00 ± 2.50	19.83 ± 2.23	1.83 ± 3.20	0.5664
Litter cover [%]	2018	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.0000
	2019	2.51 ± 0.56	2.11 ± 0.78	-0.41 ± 0.38	0.5361
	2020	7.42 ± 0.74	6.83 ± 0.67	-0.58 ± 0.80	0.4650
Vegetation height [cm]	2018	-	-	-	-
	2019	70.44 ± 2.23	60.59 ± 2.82	-9.85 ± 4.05	0.0151
	2020	47.51 ± 2.27	55.78 ± 3.89	8.40 ± 4.43	0.0511

Table E. 3: Effects of spontaneous vegetation of vineyard sites on local vegetation parameters (N = 3). LMMs were used with 'site' as a random factor. Different letters indicate significant differences between treatments ($p < 0.05$).

	Year	Vineyard A	Vineyard B	Vineyard C
Vegetation cover [%]	2018	70.00 ^a ± 5.77	25.00 ^b ± 10.41	46.67 ^a ± 9.27
	2019	71.67 ± 6.00	45.00 ± 15.00	70.00 ± 7.63
	2020	69.17 ± 0.83	63.33 ± 4.41	63.33 ± 4.41
Bare ground cover [%]	2018	30.00 ^b ± 5.77	75.00 ^a ± 10.41	56.67 ^b ± 11.67
	2019	13.33 ± 1.67	55.00 ± 15.00	30.00 ± 7.64
	2020	16.67 ± 3.33	30.00 ± 2.89	18.33 ± 4.41
Herb cover [%]	2018	76.67 ± 13.33	95.00 ± 0.00	60.00 ± 17.32
	2019	75.00 ^{ab} ± 10.41	93.33 ^a ± 3.33	46.67 ^b ± 8.82
	2020	71.67 ^a ± 7.26	90.00 ^a ± 2.89	13.33 ^b ± 3.33
Grass cover [%]	2018	23.33 ± 13.33	5.00 ± 0.00	40.00 ± 17.32
	2019	25.00 ^{ab} ± 10.41	6.67 ^b ± 3.33	53.33 ^a ± 8.82
	2020	28.33 ^b ± 7.26	10.00 ^b ± 2.89	86.67 ^a ± 3.33
Litter cover [%]	2018	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	2019	13.23 ^a ± 7.64	0.00 ^b ± 0.00	0.00 ^b ± 0.00
	2020	10.83 ± 2.20	5.83 ± 2.20	15.00 ± 5.00
Vegetation height [cm]	2019	73.00 ^a ± 8.75	66.67 ^{ab} ± 11.02	44.40 ^b ± 8.91
	2020	54.53 ± 5.38	57.87 ± 1.64	57.00 ± 1.51

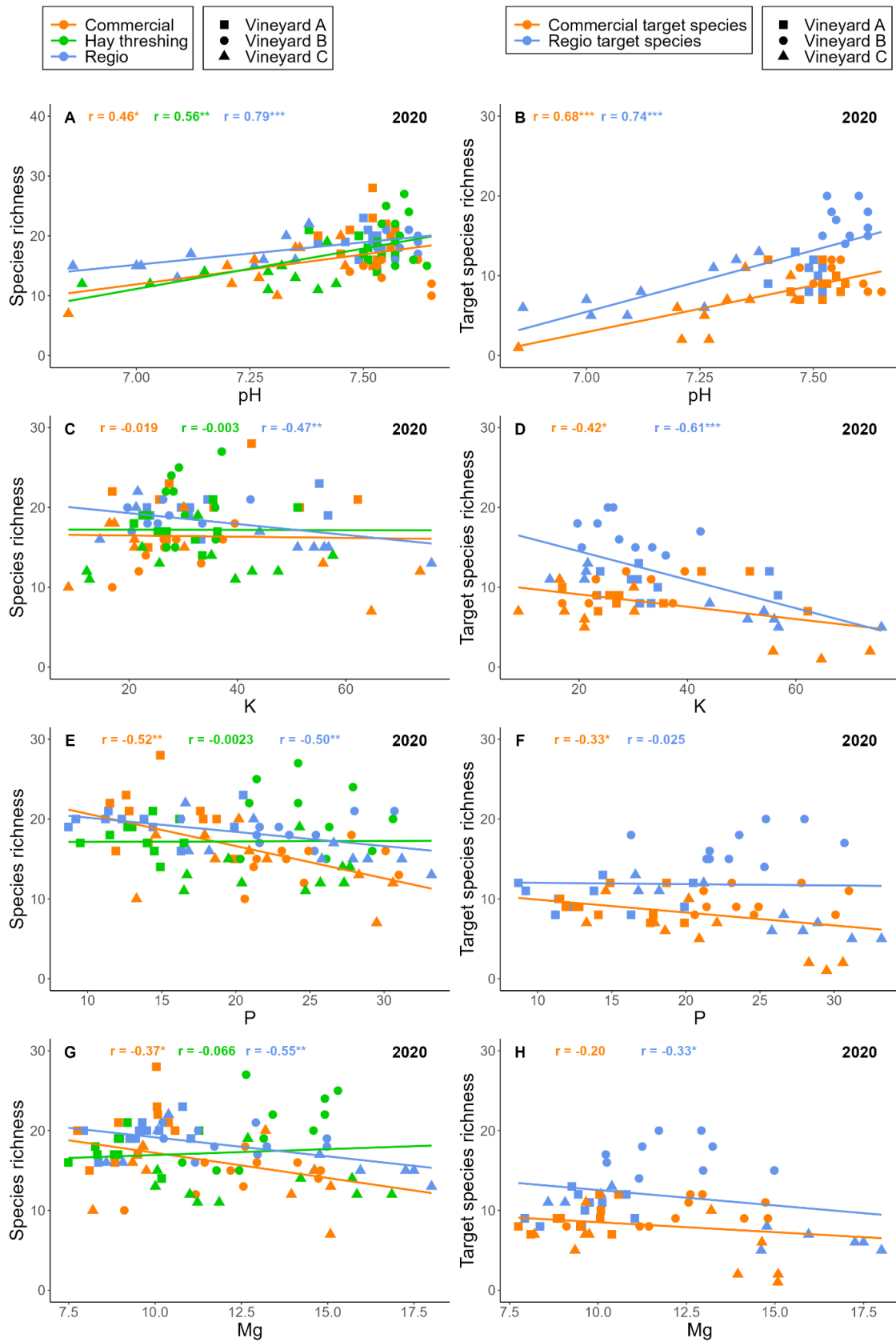


Figure E. 1: Correlation between species richness of regional mixture, commercial mixture, and hay threshing and soil parameters pH (A), K (C), P (E), and Mg (G) and target species richness of regional and commercial mixture and pH (A), K (D), P (F), and Mg (H). Pearson correlation coefficients (r) are given. Asterisks indicate significance levels ($p < 0.05 = *$, $p < 0.005 = **$, $p < 0.001 = ***$).

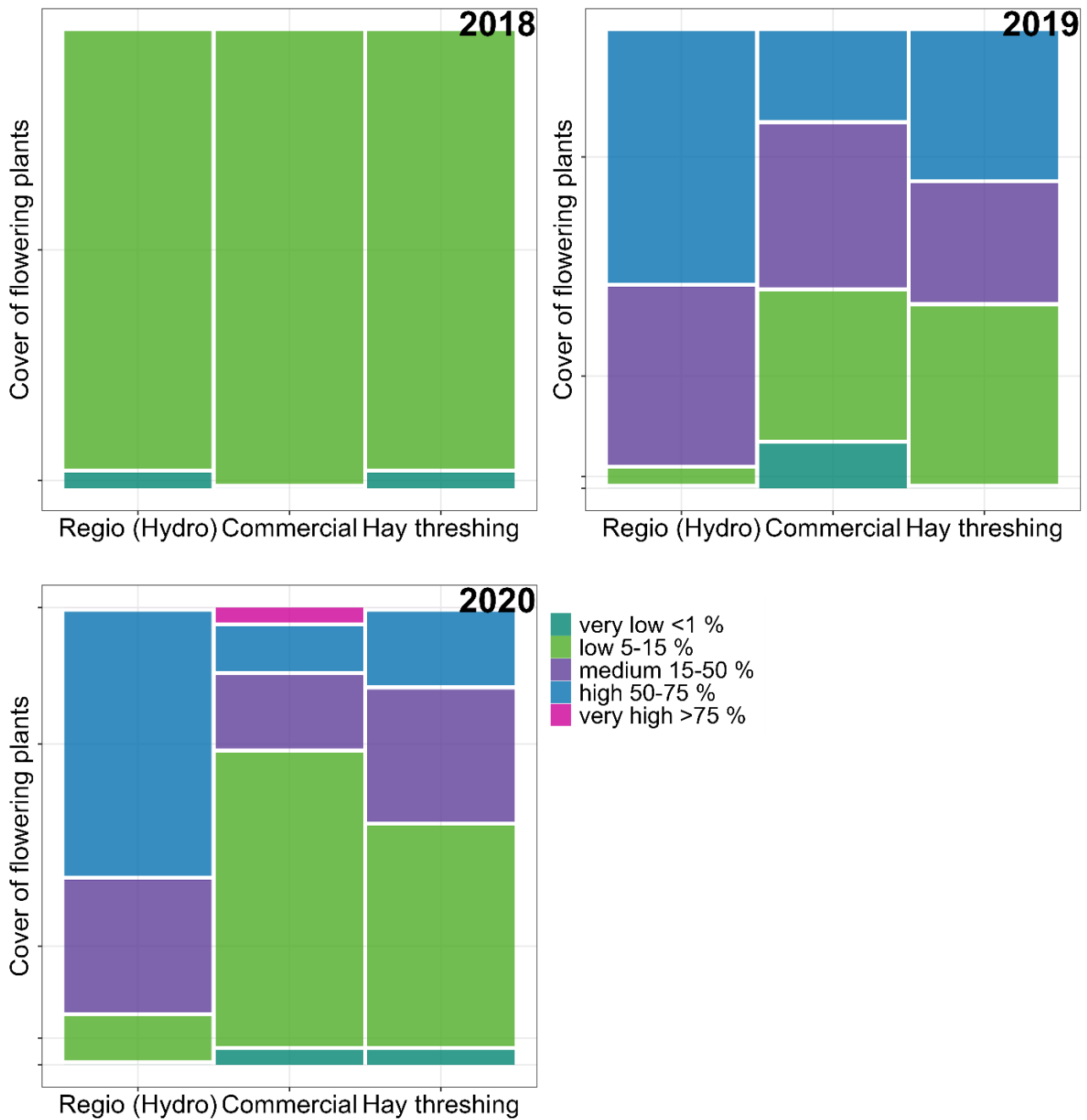


Figure E. 2: Cover of all flowering plants of different seed mixtures for 2018 – 2020. The flower coverage of all currently flowering plants was visually estimated on each sampling event in five classes (<1 % = very low; 5–15 % = low; 15–50 % = medium; 50–75 % = high; >75 % = very high).

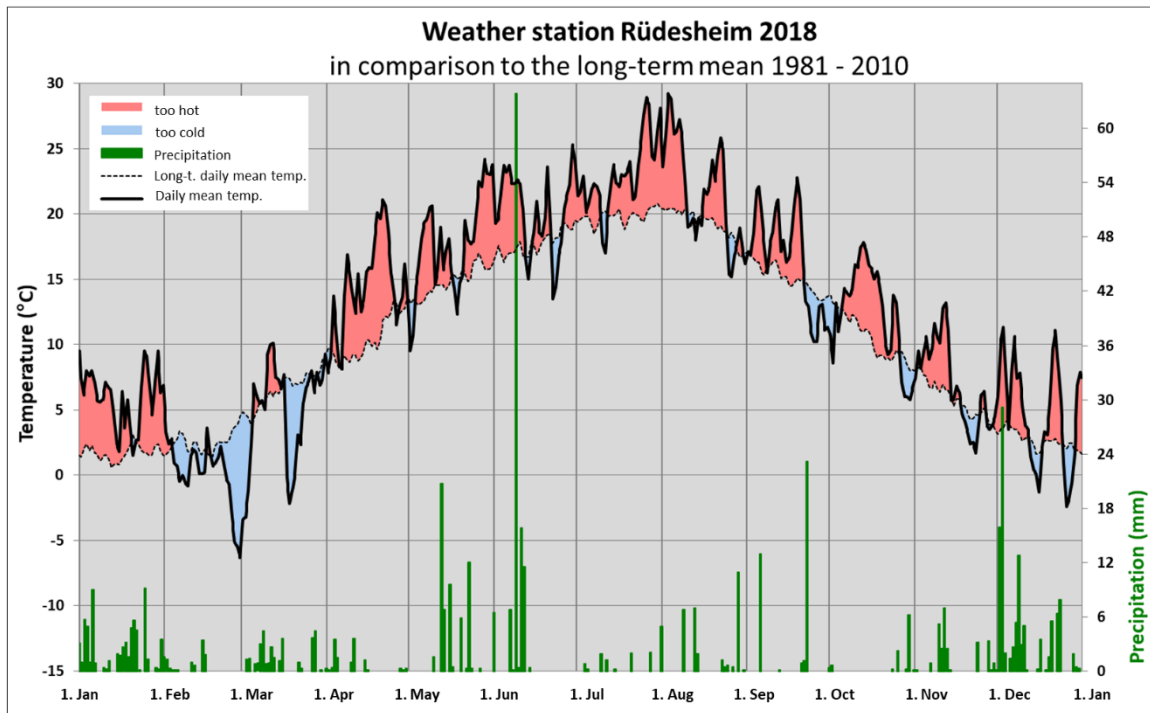


Figure E. 3: Weather data for Rüdeshheim for 2018. Black line shows daily mean temperatures and dotted black line shows long-term daily mean temperatures (1981 - 2010). Red-coloured areas represent temperatures hotter and blue-coloured areas represent temperatures cooler than the long-term daily mean temperature. Green bars show precipitation (mm).

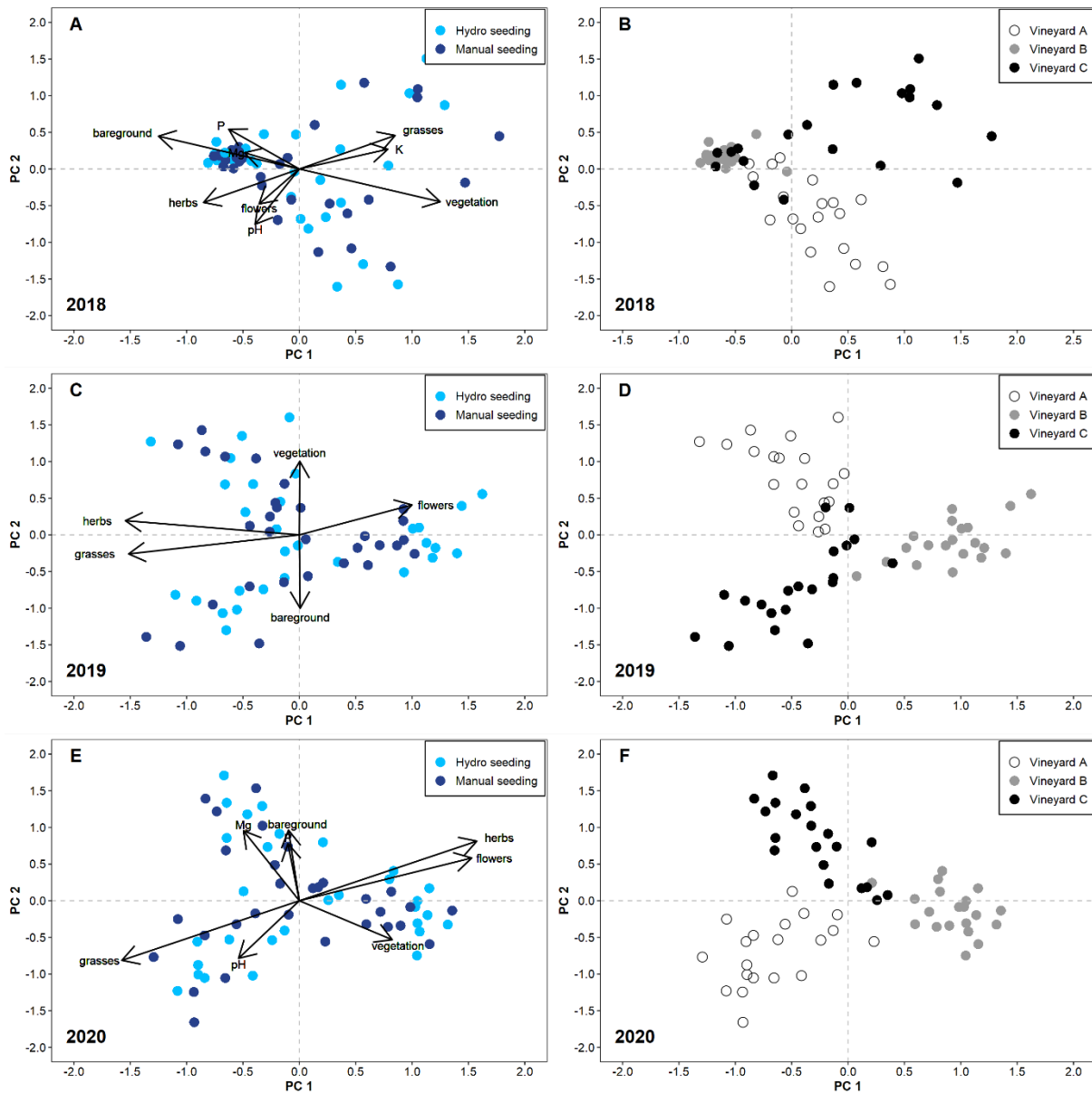


Figure E. 4: PCA results for plant species composition of seeding techniques for 2018 - 2020. Graphs show PCA scores for seeding techniques (A, C, E) and sites (B, D, F). Sample scores for hydro-seeding are displayed in light blue, and scores for manual seeding are displayed in dark blue. Site scores are displayed as white (Vineyard A), black (Vineyard B), and blue (Vineyard C) dots. Environmental parameters that were significantly related to the PCA axes ($p < 0.05$, 9999 permutations) were included post-hoc by projection.