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Multi-taxa responses to forest disturbances through a multi-disciplinary approach

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Coordinator: Prof. Claudio Bonghi
Supervisor: Prof. Lorenzo Marini
Co-Supervisors: Prof. Andrea Battisti
Dr. Cristiano Vernesi
Dr. Duccio Migliorini

Ph.D. student : Davide Nardi

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Padua, 29 September 2022 Davide Nardi

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Summary

Natural disturbances, such as windstorms and insect outbreaks, are complex phenomena with multiple effects on forest ecosystems. Unfortunately, these disturbances are expected to increase in the coming years, due to the climate change. Therefore, understanding the multi-facet impacts of forest disturbances is an urgent objective for targeting appropriate management strategies. During my PhD thesis, I focused on three main goals: (I) understanding the effects of a large-scale wind disturbance on forest biodiversity, (II) identifying the predisposing factors for the tree susceptibility to bark beetle attacks, and (III) evaluating the ecological role of post-disturbance sites to protect biodiversity at the landscape scale.

In the first part of the thesis, I focused on the effects of wind disturbance on three groups of organisms: ground-dwelling arthropods, microarthropods, and oomycetes. Our results highlighted that wind disturbance had different consequences depending on the taxonomic and the functional traits. Moreover, underlying ecological gradients, such as topography and climate, modified the impact of windstorm. In particular, we found that stronger impacts usually occurred at high elevations and drier sites.

In the second part, I studied biotic disturbances focusing on the predisposing factors of the European spruce bark beetle (*Ips typographus* L.) outbreaks. Both local growing conditions of trees and landscape features are important predictors of the risk of bark beetle outbreaks. At the early stage of a large-scale outbreak, forest stands on flat terrains with high water availability, and high host cover exhibited the highest high-risk of attack.

In the third part, I focused on the long-term response of post-disturbance sites. Using spiders as target group, we found that temporary abandoned patches played a pivotal role in enhancing the spider diversity at the landscape scale. These transition habitats created by disturbance or abandonment enhanced the landscape environmental heterogeneity providing novel ecological niches compared to homogenous forest landscapes.

Overall, two general conclusions can be derived from this thesis. First, since forest disturbances are extremely complex phenomena, studying the interactive effects between disturbance and underlying ecological gradients might help to successfully understand the impact of these natural processes. Second, because forest disturbances are multifaced events affecting both biotic and abiotic dimensions of forest ecosystems, complementary skills are needed to study them. Here, we suggested that different investigation approaches should be used depending on the spatio-temporal scale and the target organisms. Finally, the high complexity

of such phenomena and the variety of their outcomes should be considered when designing conservation and management actions, and when planning future forest landscapes. In conclusion, my PhD work contributed to emphasise the urgent need for a multidisciplinary and a holistic approach to shape more resilient forests under global change.

Riassunto

I disturbi naturali, come i danni da vento e le epidemie di insetti fitofagi, sono fenomeni complessi, che possono avere molteplici effetti sugli ecosistemi forestali e che sono destinati ad aumentare nei prossimi anni a causa del cambiamento climatico. Pertanto, la comprensione dei loro effetti sull'ecosistema è un obiettivo essenziale nella ricerca scientifica e condizione imprescindibile per implementare corrette strategie di gestione. Durante la mia tesi di dottorato mi sono concentrato su tre obiettivi principali: (I) comprendere gli effetti di un disturbo da vento a larga scala sulla biodiversità forestale, (II) capire i fattori predisponenti la suscettibilità degli alberi alle epidemie di bostrico tipografo e (III) studiare il ruolo ecologico dei siti post-disturbo a scala di paesaggio nella conservazione della biodiversità.

Nella prima parte della tesi, mi sono concentrato sugli effetti del disturbo da vento su tre gruppi di organismi: artropodi camminatori, microartropodi e oomiceti. Le ricerche condotte hanno evidenziato che lo stesso disturbo può avere conseguenze diverse a seconda delle caratteristiche tassonomiche e funzionali degli organismi. Inoltre, i gradienti ecologici preesistenti, come la topografia e il clima, interagiscono con il disturbo forestale modificando l'impatto degli schianti da vento. In particolare, si è riscontrato che la perturbazione delle comunità è maggiore in quelle condizioni già critiche, come le alte quote e i siti siccitosi.

Nella seconda parte della tesi, ho studiato i disturbi biotici concentrandomi sui fattori predisponenti le epidemie del bostrico dell'abete rosso (*Ips typographus* L.). Sia le condizioni di crescita degli alberi che le caratteristiche del paesaggio sono fattori importanti per il rischio di attacchi da parte degli scolitidi. Nella fase iniziale di una infestazione a larga scala, la bassa quota, i terreni pianeggianti con un'elevata disponibilità di acqua e un'alta copertura di boschi puri di abete determinano condizioni di alto rischio.

Nella terza parte della tesi, mi sono concentrato sulla risposta a lungo termine dei siti post-disturbo. Utilizzando i ragni come gruppo studio, abbiamo osservato che le zone abbandonate in via di riforestazione svolgevano un ruolo fondamentale nel migliorare la diversità di questi predatori a scala di paesaggio. Questi habitat transitori creati dal disturbo o dovuti all'abbandono aumentano l'eterogeneità ambientale fornendo maggiori nicchie ecologiche rispetto ad altri habitat più omogenei.

Nel complesso, dalla mia tesi si possono trarre due conclusioni generali. In primo luogo, poiché i disturbi forestali sono fenomeni estremamente complessi, lo studio degli effetti di interazione con i gradienti ecologici preesistenti può aiutare a comprendere meglio i processi naturali. In secondo luogo, poiché i disturbi

forestali sono eventi compositi, sono necessarie competenze complementari. In questo caso, l’utilizzo di diversi approcci di indagine a seconda della scala spaziale/temporale e dell'organismo target, ha permesso di studiare in modo più comprensivo i fenomeni. L'elevata complessità di questi eventi e la varietà dei loro effetti dovrebbero essere presi in considerazione quando si effettuano azioni volte alla conservazione e alla gestione degli ecosistemi, o si pianificano i paesaggi forestali. In conclusione, il mio lavoro di dottorato ha contribuito a sottolineare l'urgente necessità di un approccio multidisciplinare e olistico per creare foreste più resilienti ai cambiamenti a scala globale.

INTRODUCTION

Natural disturbances in forest ecosystems

In ecology an environmental disturbance can be defined as "any relatively discrete event that disrupts the structure of an ecosystem, community, or population, and changes resource availability or the physical environment" (Pickett and White 1985). Several natural disturbances, such as landslides, fires, windstorms, insect and pathogen outbreaks, play a decisive role in forest ecosystem dynamics worldwide (Schelhaas *et al.* 2003, Senf and Seidl 2021, Viljur *et al.* 2022). Depending on the causal agents, natural disturbances can be divided into two main categories: abiotic and biotic disturbances. On the one hand, abiotic disturbances are characterised by a faster impact on forest ecosystems, even though they may have very different effects depending on the scale (Moore and Allard 2011). Among the others, wind is one of the most important causes of forest loss in temperate forests (Gardiner *et al.* 2010, Seidl *et al.* 2014). On the other hand, biotic disturbances, such as insect or pathogen outbreaks, can change forest structure due to a subsequent tree mortality, which is dependent on infestation patterns and dynamics (Weed *et al.* 2013, Kautz *et al.* 2017). In the last decades, insect outbreaks severely hit forests worldwide causing strong impacts on ecosystem services, economic losses, and environmental changes (Hlásny, Zimová, *et al.* 2021, Marini *et al.* 2022).

Catastrophic disturbances are generally considered as economic issues due to their impact on ecosystem services such as carbon stocks and timber productivity (Thom and Seidl 2016). Large, extensive, and frequent disturbances can also dramatically modify forest landscapes by replacing semi-natural forests with more homogeneous land uses (Ibarra and Martin 2015, Roeder *et al.* 2018, Chen *et al.* 2021). However, from an ecological perspective, even catastrophic events might play an important role in forest regeneration shaping future forest landscapes (Seidl *et al.* 2022, Viljur *et al.* 2022). Climate change is expected to increase the risk of natural disturbance worldwide, and large-scale disturbance events are expected to be more frequent than in the past (Seidl and Rammer 2017, Seidl *et al.* 2017, Albrich *et al.* 2020, Senf and Seidl 2021). Thus, a deeper scientific-based knowledge of the consequences on forest ecosystem is urgently needed to cope with future challenges in landscape management and biodiversity conservation (Forzieri *et al.* 2021).

Windstorms and their effects on forest biodiversity

Wind disturbance is one of the most important abiotic natural disturbances in forest ecosystems, accounting for more than 50% of the total amount of forest damage in Europe (Gardiner *et al.* 2010, Seidl *et al.* 2014). Scientific literature clearly showed that the probability of windstorm occurrence has largely increased in the last decades (Gregow *et al.* 2017, Senf and Seidl 2021). Due to climate change, increasing frequency and magnitude of windstorms are expected in the coming years, especially in coniferous forests (Seidl *et al.* 2017). Nevertheless, looking at windstorms as only exceptional and catastrophic phenomena is misleading, because wind disturbance is known as an important natural driver of ecosystem processes and forest succession (Ulanova 2000, Panayotov *et al.* 2011, Meigs *et al.* 2017). Ecological effects of windstorms include multi-scale outcomes such as increasing landscape heterogeneity, enhancing forest structure, influencing species composition, and inducing evolutionary processes (Lugo 2008).

Direct effects of windstorm at the local scale

In forests, natural disturbances caused severe changes in environmental conditions, such as canopy opening, soil and abiotic parameters alteration. On the one hand, small scale habitat heterogeneity increases niche availability and provides novel resources often enhancing community diversity (Bouget and Duelli 2004, Wermelinger *et al.* 2017a).Windstorms lead to changes at different spatial scales, ranging from the single tree (i.e. treefalls) to the stand (i.e. windthrow) scale (Bouget and Duelli 2004). Deadwood amount and diversity (e.g. logs, snags, and stumps) increase thus providing new resources for a wide range of organisms such as lichen, fungi, saproxylic beetles, birds, and mammals (Radu 2006, Lassauce *et al.* 2011, Bouget *et al.* 2014, Uhl *et al.* 2022). Due to canopy removal, radiation suddenly increases and moisture decreases in windfalls in the short-medium term (Gray *et al.* 2002, Vilhar *et al.* 2015). Furthermore, since canopy removal and abiotic changes trigger herbaceous vegetation renewal by modifying the litter surface and resource availability even in the short term (Ulanova 2000, Cacciatori *et al.* 2022), new insect species and other invertebrates might take advantage of these new conditions. In particular, windstorms lead to direct and indirect effects on soil and litter thus deeply altering soil-inhabiting microarthropod communities (Bouget and Duelli 2004, Čuchta *et al.* 2012, Sterzyńska *et al.* 2020, Wehner, Simons, *et al.* 2021).

Managing windthrow areas is often a complex task because many conflicting interests intersect such as pest management, tourism, wood production, and biodiversity conservation (Hlásny, König, *et al.* 2021). Besides natural consequences of windstorms, salvage logging is usually performed in post-disturbance management to prevent bark beetle outbreaks and save economically valuable timber (Dobor *et al.* 2020a, 2020b). Salvage logging represents an additional anthropic disturbance on forest ecosystems affecting forest functionality and biodiversity (Leverkus *et al.* 2021). Indeed, to preserve at least 90% of forest-living species about 75% of windthrow areas should be unlogged (Thorn *et al.* 2020). Disentangling the effects of windstorm and salvage logging on forest biodiversity is challenging and the response might depend on the considered taxa. For instance, previous studies highlighted the negative effect of salvage logging on deadwood-related taxa (i.e. saproxylic fungi and insects) due to the removal of deadwood amount and diversity with opposite effects on ground-dwelling arthropods, such as ground beetles and spiders (Wermelinger *et al.* 2017a, Thorn *et al.* 2018, Georgiev *et al.* 2021), and flower visiting insects, such as pollinators and other flying insects (Rodríguez and Kouki 2017, Wermelinger *et al.* 2017a), which increased in post-disturbance sites. Moreover, Lain *et al.* (2008) showed that birds were negatively affected by salvage logging, whereas within unlogged sites the effect of wind disturbance alone promoted species richness. Hence, the same disturbance effect may have different outcomes depending on the taxa considered. Although different approaches aimed at mitigating the negative effect of salvage logging on biodiversity (Thorn *et al.* 2017a), the compromise between pest prevention and conservation purposes is still difficult, especially in areas with restricted accessibility. Post-disturbance intervention strategies should be deeply evaluated by considering local conditions, in spite of possible negative effect of salvage logging to the forest landscape.

Direct effects of windstorm at the landscape scale

Windstorm and salvage logging effects on biodiversity, occur even at large spatial scale through the alteration of composition and configuration of forest landscape (Turner 2010, Turner and Gardner 2015). Usually the higher complexity in post-disturbance areas can influence patch diversity and connectivity as well as the different temporal progression of forest succession in disturbed sites can promote the creation of ecotones. These new conditions lead to an increase of resource availability for a wide range of organisms by providing novel habitats (Turner 2010, Kark 2013, Schindler *et al.* 2013). For instance, previous studies on temperate forest ecosystems highlighted the role of spatial heterogeneity in enhancing communities of arthropods (Oxbrough *et al.* 2010, Gossner *et al.* 2013, Barbaro *et al.* 2016) and vertebrates (Carey and Wilson 2001, Barbaro *et al.* 2016, Klingbeil and Willig 2016). Also, heterogeneity might occur at smaller scale since biological legacies might contribute to increase landscape mosaic heterogeneity in post-harvesting plots in the long term (García-Tejero *et al.* 2018). Mosaic of logged, unlogged and residual forest patches might have great potential in sustaining biodiversity (Wermelinger *et al.* 2017a).

Potential interactions between forest disturbance and underlying ecological gradients

Traditionally, ecological studies on natural disturbances were mainly focused on the main effect of disturbance or on the comparison between different post-disturbance treatments (e.g. Bouget and Duelli 2004a, Larrivée *et al.* 2005, Buddle *et al.* 2006, Gandhi *et al.* 2008, Renčo *et al.* 2015, Wermelinger *et al.* 2017). Little attention has been paid to the potential interacting effects of disturbance and pre-existing underlying ecological factors, such as elevation or slope gradient (Haugo *et al.* 2010).

The most important ecological gradients in biodiversity pattern in mountain areas are topography and climate (Vetaas *et al.* 2019). Although elevation covaries with many other variables, the change in temperature seems to be the most relevant component explaining the biological patterns (Peters *et al.* 2016). Other important topographic gradients are slope and aspect. Slope is one of the most important predictors of soil moisture (Penna *et al.* 2009), while aspect is related to the different sun-exposure of sites (Prévost and Raymond 2012). Gradients of slope, aspect, and elevation and their interactions might drive changes in mountain vegetation communities (Bruun *et al.* 2006, Åström *et al.* 2007, Stage and Salas 2007), as well as in insect communities (Johansson et al. 2017). Large-scale disturbance events represent an opportunity for ecologists to uncover the potential interactive effects between disturbances and underlying ecological gradients. There are two different ways in which disturbance can affect biological responses along an ecological gradient (Fig. I). First, the effect of disturbance and other environmental gradient can be additive, thus showing the same effect size. Second, disturbance can interact with the ecological gradient in mediating the biological response, e.g. under certain conditions the overall effect of disturbance is weaker, in others is stronger. Understanding under which conditions forests are more sensitive to disturbance is of pivotal importance for improving forest management and conservation actions.

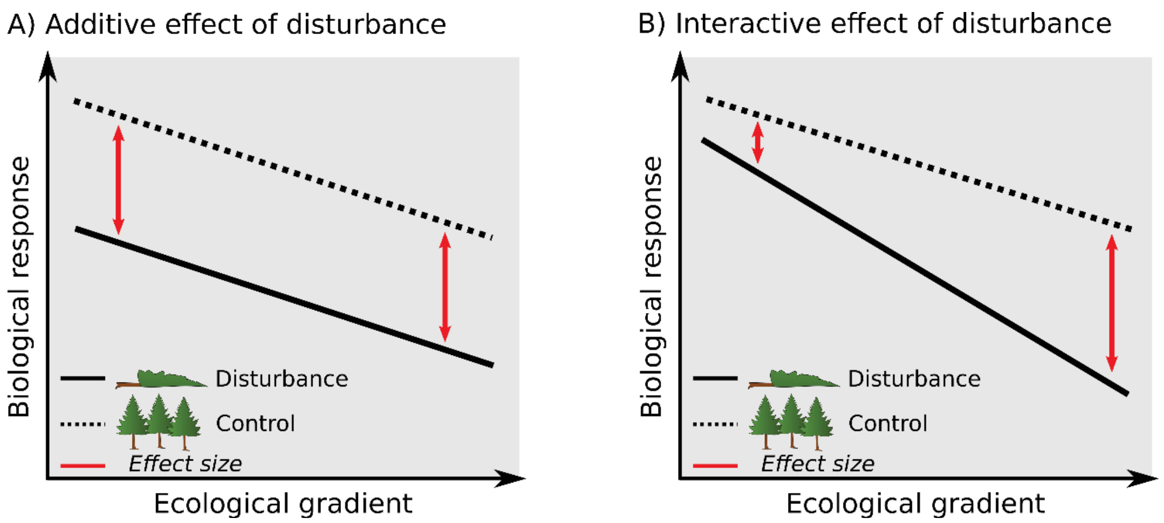

Figure I - Examples of additive (Fig. I A) and interactive (Fig. I B) effects in the context of forest disturbance along an underlying ecological gradient.

Investigating soil forest communities

Wind disturbance and salvage logging lead to significant changes in forest soil ecosystems. Because of this compounded disturbance, ground-living organisms can be severely affected in post-disturbance sites. However, effects of forest disturbances might depend on the different functional traits and organism preferences. For instance, niche preferences and dispersal abilities are important drivers of community composition (Hirao et al. 2008). Here, we assessed the effect of wind-induced soil disturbance on three groups of organisms with different ecology, biological cycles, habitat preferences, and dispersal strategies: ground-dwelling arthropods, microarthropods, and Oomycetes.

Ground-dwelling arthropods include different groups of insects and arachnids. We focused on ground beetles (Coleoptera, Carabidae), spiders (Araneae), and harvestmen (Opiliones). These groups were selected because they exhibit different mobility, habitat specialization and hunting strategies with communities occurring both in forest and open semi-natural habitats (Gerlach et al. 2013). Ground beetles have been widely used as bioindicators and environmental quality assessment (Rainio and Niemelä 2003, Pearce and Venier 2006) and they include species with different dispersal strategies (i.e. macropterous and brachypterous species). Spiders and harvestmen are important predators among forest arthropods and they respond well to habitat changes due to their narrow environmental preferences (Pearce and Venier 2006, Pinto-da-rocha et al.

2007). In particular, spiders show a wide range of ecological niches and dispersal strategy, i.e. dwelling and ballooning (Bonte et al. 2003).

Micro-arthropods are small epigeic and edaphic organisms. Springtails (Collembola) and soil mites (orders Sarcoptiformes, Mesostigmata, Trombidiformes) are key functional groups involved in organic matter decomposition and nutrient recycling (Seastedt 1984). Moreover, microarthropods contribute to sustain food webs being prey of other arthropods, i.e. ground beetles, spiders, and harvestmen (Ferguson and Joly 2002). Springtails and soil mites are highly-diverse groups including many species with different feeding and environmental preferences (Behan-Pelletier 1999, Salmon and Ponge 2012). Most of the published literature on wind disturbance focused on the major groups of vertebrates and invertebrates (Bouget and Duelli 2004, Bouget 2005, Thorn *et al.* 2017a), while effects on micro-arthropods are still poorly studied.

Oomycetes are a group of eukaryotic micro-organisms, mainly living in soil and freshwater habitats. Oomycetes are ubiquitous in soils and they could play an important role in organic matter decomposition and nutrient recycling (Kramer et al. 2016). However, many lineages of oomycetes include plant pathogens and saprophytes, such as Peronosporales (Thines 2014). Pythiaceae is the most important family of soil-born plant pathogens including some genera of great importance for forest ecosystems, i.e. *Pythium* and *Phytophthora* (Thines 2014, H Ho 2018). Besides few aggressive species have been deeply studied, the occurrence of oomycete communities in forest soil and effects of soil disturbances remain mostly unknown (Coince et al. 2013).

DNA-metabarcoding as novel technique for community ecology studies

Since many of soil-inhabiting groups are quite difficult to study because of small size (e.g. unicellular organisms) or because they need high taxonomic expertise and time-consuming identification, molecular approach can provide useful tools to unravel this high biodiversity hidden in the forest litter. Recently, the availability of HTS (High Throughput Sequencing) allowed producing billions of DNA reads per single experiment. Thus, mixtures of amplicons (amplified target-DNA fragments) from different species can be analysed at once and this approach is called DNA metabarcoding. DNA-metabarcoding, hereafter metabarcoding, allows to analyse a collections of organisms (bulk sample) or environmental DNA (eDNA) sample by using universal PCR primers to mass-amplify a taxonomically informative target gene (Yu *et al.*

2012). Output sequences need to be processed with bioinformatic pipelines to retrieved final sequences that can be referred to a single species or haplotype: OTUs (Operational Taxonomic Units) or ASVs (Amplicon Sequence Variants) by using clustering or denoising approaches, respectively. Depending on the type of the sample and/or the organism, DNA-metabarcoding approach can be applied to a community DNA, i.e. bulk sample of collecting target organisms, or an environmental sample (eDNA), i.e. raw matter containing DNA, such as extracellular DNA and microscopic living organisms. Thanks to the possibility of analysing the entire DNA sample at once, metabarcoding approach allows to answer ecological questions and build up large-scale monitoring programs, becoming an useful tool in environmental research (Taberlet *et al.* 2012, Ji *et al.* 2013).

Compared to the conventional morphological identification, metabarcoding approach has advantages and disadvantages. A common issue in metabarcoding is selecting the target gene and primers for PCR-amplification. Each target gene (generally 18S and COI for animals) might work better with some groups rather than others (Elbrecht *et al.* n.d., Cowart *et al.* 2015). Thus, selecting good primers is a crucial step (Liu *et al.* 2020). Primers are often not fully exclusive and several no-target groups might be amplified during PCR step (Pérez-Burillo *et al.* 2022) or preferential amplification biases might occur (Krehenwinkel *et al.* 2017). Moreover, metabarcoding needs bioinformatic skills and computer computations are often time-consuming (Coissac *et al.* 2012). Although, many new bioinformatic tools and approaches flourished in the last years (Bolyen *et al.* 2019, Brandt *et al.* 2021, Mathon *et al.* 2021), parameter tuning by bioinformaticians is often required. Taxonomic identification can be inferred by matching the output sequences with those of a sequence reference database, so taxonomic depth is restricted and strongly depends on the reference database coverage and completeness of each group (Watts *et al.* 2019). For instance, large-scale monitoring surveys in poor-known ecosystems, such as soils, revealed large amount of unidentified invertebrate OTUs (Dopheide *et al.* 2019). Finally, metabarcoding-derived data should be treated as qualitative (presence/absence), or at most as semi-quantitative. Indeed, a number of potential biases might be introduced in the process, such as variable cell quantity in different tissues, different DNA extraction success, different amplification rate, and different quantitative estimates among sequencing runs (Lamb *et al.* 2019).

On the other hand, metabarcoding provides several advantages compared to conventional approaches. Since metabarcoding is based on DNA-barcode approach, different species can be discriminate due to their different DNA, rather than conventional morphological traits. Metabarcoding might up-scale similar advantages of molecular taxonomy: detecting cryptic species (De Luca *et al.* 2021), real estimates of the diversity of hyper-diverse groups as Hymenoptera (Dopheide *et al.* 2019, Sire *et al.* 2022) or poor-known groups such as marine Annelida (Cowart *et al.* 2015), and identifying species regardless of their developmental stage (Jalali *et al.* 2015). Costs of time in collecting data from field and processing samples are similar between metabarcoding and conventional sampling (Watts *et al.* 2019). However, in morphological identification the taxonomic skills are often group-specific and studies with wide taxonomical-range are quite rare (e.g. Peters *et al.* 2016). On the contrary, metabarcoding requires bioinformatic skills which can be used for several taxonomic groups. Nevertheless, taxonomist expertise is still fundamental to improve knowledge of studied systems, which cannot be investigated by solely molecular approaches, and increase sequence reference databases.

Bark beetles: the most important biotic disturbance in spruce forests

Abiotic disturbance, such as windstorm or heat wave and drought, might also trigger biotic disturbances such as pest outbreaks (Stadelmann *et al.* 2014, Havašová *et al.* 2017, Marini *et al.* 2017, Netherer *et al.* 2019, Koontz *et al.* 2021). Recently, bark beetle outbreaks strongly impacted coniferous forests worldwide by leading to unprecedented tree mortality (Hlásny, Zimová, *et al.* 2021), and by expanding outside their historical range distribution (Raffa *et al.* 2008). Large outbreaks are expected to increase in the future due to climate change, or by interaction with other forest disturbances (Jönsson *et al.* 2009, Bentz and Jönsson 2015, Mezei *et al.* 2017, Seidl and Rammer 2017, Netherer *et al.* 2021). Bark beetle outbreaks are thus characterised by multi-dimensional outcomes: sudden carbon stock decrease, renewal process promotion, and landscape changes. From an ecological perspective bark beetles might play a pivotal role in forest ecosystems. Spots of killed trees might improve the forest succession, providing more suitable habitat for several species, as well as increasing the amount of dead-wood (Zeppenfeld *et al.* 2015, Kortmann *et al.* 2018). Similarly to windstorm canopy removal effect, these new open habitats are expected to become transitional patches within the landscape, thus enhancing the diversity at the landscape scale and sustaining rich communities (Hilmers *et al.* 2018). Besides possible positive effects, during massive outbreaks forest habitat can be completely removed changing the landscape and causing the loss of forest specialists. For these reasons, monitoring of bark beetle-induced tree mortality is a fundamental goal in forest and landscape management.

In Europe, the European spruce bark beetle *Ips typographus* L. (Coleoptera: Curculionidea) represents one of the most important forest pest causing huge impacts on the forest landscape and affecting economic and ecological dimensions of forest ecosystem (Hlásny, König, *et al.* 2021, Hlásny, Zimová, *et al.* 2021). The preferential host of *I. typographus* is the Norway spruce, *Picea abies* (L.) H.Karst., and in general both healthy and weakened trees are killed after being successfully attacked (Grégoire and Evans 2007). The development of *I. typographus* depends on temperature and photoperiod and at warmer temperatures more than one generation per year might occur (Wermelinger and Seifert 1999, Netherer and Pennerstorfer 2001). Usually, under endemic phases, *I. typographus* attacks only those trees already weakened by mechanic stress or drought-induced stress. Under outbreaks, or epidemic phases, even healthy standing trees can be killed by *I. typographus* due to mass attacks (Biedermann *et al.* 2019). Triggering factors such as windstorms, heat waves, and pathogen infestations might influence the population dynamics of this insect, causing large-scale outbreaks

(Marini *et al.* 2017, Hlásny, König, *et al.* 2021). Nevertheless, scientific evidence showed a long history of epidemic phases and high tree mortality, alternated with endemic phases in forest ecosystems, thus suggesting bark beetle disturbance as an intrinsic natural disturbance of temperate forests (Økland and Berryman 2004, Čada *et al.* 2016, Kuosmanen *et al.* 2020).

Besides the economic importance, *I. typographus* should not be only described as a pest, but also as a key-stone species due to the huge effects on the forest ecosystem (Müller *et al.* 2008). The potential benefits of bark beetle infestations are improving forest regeneration (Zeppenfeld *et al.* 2015), increasing biodiversity (Müller *et al.* 2008, Beudert *et al.* 2015, Kortmann *et al.* 2021), and providing habitat for flag-species (Kortmann *et al.* 2018). Thus, management strategies should be carefully considered during outbreaks, especially in protected areas (Kortmann *et al.* 2021). For that reason, post-outbreak management is challenging, and it can be seen as a continuum between wood production and ecosystem conservation (Hlásny, König, *et al.* 2021). Monitoring and mapping infestations are crucial points in forest management: understanding infestation patterns allows selecting high-priority zones for interventions as well as no-intervention areas.

Tree mortality predisposing factors often occur at different spatial scales, from individual/local factors to stand or landscape features. Small-scale factors are often based on individual traits of beetles or host trees. On the one hand, synchrony of adult emergence (which is important to mass attacks), and perceptual range and energetic level of insects (which affect the dispersal and the host searching activities) are important individual traits of beetles (Kautz *et al.* 2014). On the other hand, tree susceptibility depends on multiple factors, and the potential of individual trees in inducing defence compounds might play a pivotal role in inhibiting mass attacks (Schiebe *et al.* 2012). Drought stress is a well-known predisposing factor since acute water deficit might affect the defence response of the host tree (Netherer *et al.* 2015, 2019, 2021, Matthews *et al.* 2018). Other small scale factors affecting tree resistance are soil properties (Dutilleul *et al.* 2000, Netherer and Nopp-Mayr 2005, Blomqvist *et al.* 2018), local topography (Blomqvist *et al.* 2018), sun-exposure of host tree (Kautz *et al.* 2013), and structural and anatomical properties (Baier 1996). However, outbreak-triggering factors usually act at larger spatial scale: windthrows or large-scale drought-stress are the most important factors prompting an epidemic phase (Økland and Berryman 2004, Marini *et al.* 2017). Windstorms create a high availability of mechanically damaged trees (i.e. uprooted or broken trees), which contribute to feed local bark beetle populations (Bouget and Duelli 2004, Temperli *et al.* 2013, Stadelmann *et al.* 2014, Potterf *et al.* 2019, Nardi, Finozzi, *et al.* 2022). Outbreaks are also characterised by high spatial dependency from bark beetle sources within the landscape (Økland *et al.* 2016, Seidl *et al.* 2016). Moreover, landscape features, such as landscape composition and configuration might play an important role in spreading infestations at large scale. The number of coniferous patches, as well as host connectivity, together with local predisposing factors, can drive regional scale outbreaks (Gilbert *et al.* 2005, Seidl *et al.* 2016). Also, previous studies showed that increased forest composition diversity can decrease infestation risk (Zhang and Schlyter 2004, Kärvemo *et al.* 2016, Berthelot *et al.* 2021). Finally, interacting cross-scale effects between triggering factors might boost large-scale bark beetle outbreaks, in particular under climate change (Temperli *et al.* 2013, Jaime *et al.* 2022).

Forest managers need predictive models as well as large-scale monitoring program to manage bark beetle outbreaks. Different models and frameworks predicting bark beetle risk have been developed to cope with the needs of operational tools in forest management (Netherer and Nopp-Mayr 2005, Stadelmann *et al.* 2013). However, more evidence and new field data need to be collected to validate and improve the risk assessment, as well as near real-time monitoring. Pheromone traps or tree baiting traps might play an important role in detecting exceeding thresholds of bark beetles population or in understanding phenological patterns (Weslien *et al.* 1989). However, such tools are not feasible to large-scale continuous monitoring programs, since many conditions (e.g. temperature, wind, host presence) can affect the trap efficiency as well as the distance (Duelli *et al.* 1997, Wermelinger 2004, Hinze and John 2020). Other tools, such as remote sensing, are likely to integrate classical monitoring tools and to become a standard protocol for following outbreaks at large spatial scale (Senf *et al.* 2017, Bárta *et al.* 2022).

Remote sensing represents a set of techniques dealing with aerial imagery and capable to monitor land processes (Zimmermann *et al.* 2007, Zhang *et al.* 2019). In the last years, the availability of free and medium resolution (10-20 metres of resolution) images from Sentinel 2 satellites has given the possibility of large scale surveys (Zimmermann and Hoffmann 2020). Thanks to these recent technologies, a new era of land surface monitoring has begun and many forest disturbances, such as fires, windstorms, deforestation, and pest outbreaks, can be easily mapped over large spatial extents (Lechner *et al.* 2020). Multispectral optical sensors allow combining information from different spectral bands and computing different indices, which may indicate different status of vegetation. The mapping of bark beetle tree mortality has been often based on changes in reflectance of some wavelengths thus reflecting physiological variations (Lausch *et al.* 2013, Huo *et al.* 2021). Different approach for infestation detecting can be used: change detection algorithms when time series are available, machine learning approach with single-date images, or combining both of them (e.g. Hart and Veblen 2015, Fernandez-Carrillo *et al.* 2020, Bárta *et al.* 2021). Detection is based on changes in physical properties of trees due to bark beetle attacks reflecting in different absorbance of specific length-wave bands. Depending on the time after the bark beetle attack, three main stages of tree decaying can be distinguished: green, red, and grey stages (Wulder *et al.* 2006). Green stage is the early stage, occurring in those trees having very recently been infested and whose crowns appear still green. After few weeks to several months spruce crowns start becoming reddish-brown, namely red stage. Usually red stage occurs when the beetles have already left the host tree used for breeding, but the period between the green stage and the red one strongly depends on climatic conditions, especially dryness. Grey stage appears after one to many years after the initial attack and is characterised by the loss of needles. Remote sensing detection is an important tool for infestation monitoring, but depending on the detecting stage, a time-lag exists between the beginning of the attack and the first symptom appearance, meaning that timing of the detection often does not overlap biological phases of the insect (Kautz 2014, Kautz *et al.* 2022). Furthermore, besides the promising usage of remote sensing techniques as bark beetle infestation monitoring tool, remote sensed data also provide useful large-scale datasets that might be interpreted by biological perspective and used for large-scale ecological hypothesis testing.

Research objectives and thesis structure

The general purpose of this PhD thesis is to improve our scientific knowledge about the impact of disturbances on forest biodiversity. Specifically, I aimed to test three different ecological hypotheses.

The **first part** of the thesis (Chapters I - III) deals with observational studies investigating the potential interactions between windstorm damage (and subsequent salvage logging) and underlying ecological gradients. So far scientific knowledge has investigated forest disturbances by focusing on the disturbance effects or by comparing different post-disturbance managements. However, little is known about the interacting effects of disturbances with topography, elevation, and sun-exposure. Our main hypothesis was that the effects of windstorm on forest-inhabiting communities might change depending on underlying ecological gradients and ecological traits of taxonomic groups.

In the **second part** of the thesis (Chapter IV), I focused on a biotic disturbance, i.e. bark beetles. In the case of large insect or pathogen outbreaks, interacting effects may also occur during the proceeding of forest disturbance. For instance, the different growing conditions of host trees might affect the temporal or spatial dynamics of insect infestations. We hypothesised that growing conditions and topography might influence the occurrence of bark beetle infestations.

In the **third part** of the thesis (Chapter V), I was interested in understanding the future role of the disturbed areas and the possible ecological trajectories of post-disturbance arthropod communities. However, we can only directly test the short-term effects of disturbances, because long-term responses might occur after decades since the disturbance event and no similar old forest disturbances were available. To overcome these limitations, we studied abandoned patches as proxy for post-disturbance areas. We hypothesised that these transitional patches of abandoned habitat might play a pivotal role in enhancing the overall biodiversity, by providing new habitats and resources within the forest landscape.

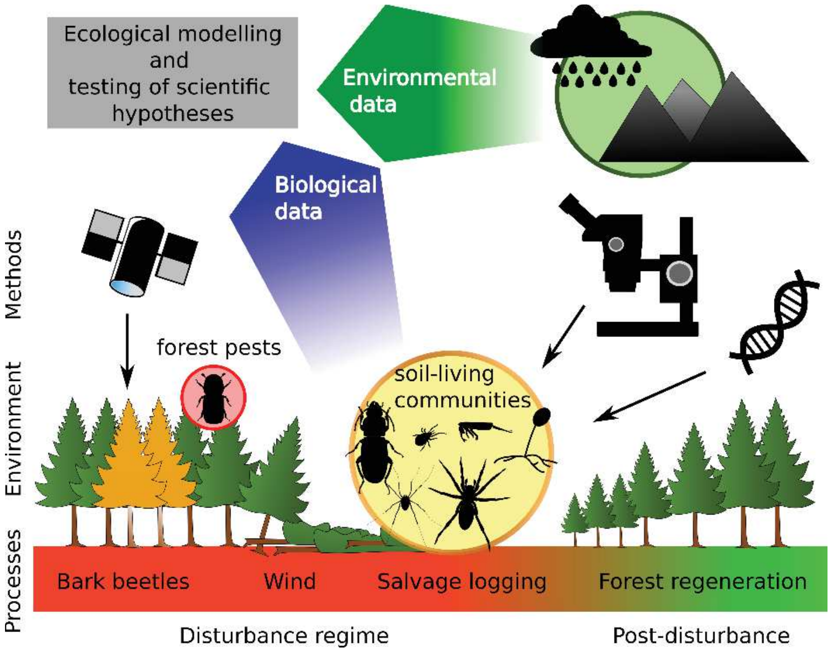

Figure II – Conceptual scheme of the PhD project. We investigated the effects of abiotic (i.e., windstorm) and biotic (i.e., bark beetle outbreak) disturbances on the forest ecosystem. We used different approaches depending on the scales and target organisms: traditional arthropod sampling, remote sensing, DNA-metabarcoding, and landscape ecology. Interactions with underlying environmental gradients was a key-point in this project.

The chapters of the thesis are described in detail below.

- **Chapter I: Short-term response of ground-dwelling arthropods to storm-related disturbances is mediated by topography and dispersal**

  In the first chapter we showed how environmental perturbation due to windstorms and salvage logging might affect or not ground-dwelling arthropod communities of spiders (Araneae), ground beetles (Coleoptera, Carabidae), and harvestmen (Opiliones). The experiment was carried out within Parco Paneveggio -Pale di San Martino, as an observational study. Our findings suggest that the short-term response depends on topography and dispersal traits of the different groups.

- **Chapter II: Impact of forest disturbance on microarthropod communities depends on underlying ecological gradient and species traits.**

  In the second chapter we investigated the detrimental effect of windstorm and salvage logging to communities of soil microarthropods, springtails (Collembola) and soil mites (mainly

Sarcoptiformes and Mesostigmata). Thirty plots of intact forest and thirty plots of disturbed areas were sampled in paired sites. Samples were processed with a metabarcoding approach to retrieved community data. Our findings suggest that springtails and mites were strongly affected by soil disturbance and that this response might be amplified by drought conditions.

- **Chapter III: Unrevealing oomycete communities' dynamics after windstorm disturbance in alpine Norway spruce forests: A DNA-metabarcoding approach**

  In the third chapter we investigated the occurrence of oomycete communities in the soil after a windstorm event. We sampled nine plots in ten different sites by including three different habitats: intact forest, windfalls, and old clearings. Environmental DNA-metabarcoding approach was used to identify soil-living communities of oomycetes. Our findings suggest that disturbance and topography might affect the richness of oomycete communities, however, large-scale factors, such as geographic areas, are much more important than habitat type in explained species composition patterns.

- **Chapter IV: Drought and stand susceptibility to attacks by the European spruce bark beetle: A remote sensing approach**

  In the fourth chapter we used large-scale remote sensed data on bark beetle infestations in France to investigate the role of growing conditions on tree host susceptibility to bark beetles. We collected climatic, topographic, and environmental data to model the tree susceptibility to *Ips typographus* infestation under heat wave event. Our findings suggest that topography variables, such as elevation, and soil conditions, such as water availability, might interact and influence the susceptibility of spruce forest to initial bark beetle infestation.

- **Chapter V: Role of abandoned grasslands in the conservation of spider communities across heterogeneous mountain landscapes**

  In the fourth chapter we focused on the future role of transition patches between open-habitats and forest at landscape scale. A middle-term habitat in forest succession is constituted by semiopen habitat patches dominated by shrubs. These temporary patches might be derived by forest harvesting (or salvage logging) or abandonment of managed lands. We used abandoned patches as proxies to understand the long-term ecological role of post-harvesting sites in wild communities of ground-dwelling spiders at the landscape scale. We sampled six landscapes along an elevation gradient. We applied a species habitat network approach to highlight the relationships among different patches of habitats. Our findings suggest that temporary shrub-dominated patches play a pivotal role in providing resources and refugia to peculiar spider communities, thus enhancing biodiversity at regional scale.

CHAPTER I

Short-term response of ground-dwelling arthropods to storm-related disturbances is mediated by topography and dispersal

Davide Nardi, Filippo Giannone, Lorenzo Marini

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Abstract

Wind disturbances and consequent salvage logging lead to drastic changes in forest soil conditions, vegetation and microclimate, potentially affecting arthropod communities. In mountain regions, topography is expected to be particularly important to modulate the effect of canopy removal and soil disturbance potentially amplifying the ecological contrast between forest and disturbed areas. Here, we studied the short-term response of ground beetles (Carabidae), spiders (Araneae), and harvestmen (Opiliones) in wind-damaged spruce forests along statistically orthogonal gradients in elevation, slope, and aspect. We addressed three main ecological questions: (i) Does the effect of wind disturbance on diversity depend on topography? (ii) Are there specific taxon-related responses to disturbances?, and (iii) What is the role of dispersal in shaping species assembly dynamics? We generally observed that increasing slope and elevation amplified the differences between undisturbed forest and windfall areas. On the one hand, the diversity of ground beetles and harvestmen seemed to be negatively affected by wind disturbance, causing a loss of specialized forest species with a low rate of colonization of species typical of open habitats. On the other hand, several novel spider species were able to rapidly colonize windfalls and community composition strongly shifted from forest to disturbed areas. Species with long-range dispersal strategies (e.g. flying and ballooning) were those more likely to colonize windfalls. Our findings suggest that disturbance effects on ground-dwelling organisms were modulated by underlying environmental gradients and that short-term response of different taxa was dependent on their dispersal ability.

Keywords (10): Araneae, dispersal, Carabidae, ground beetles, harvestmen, Opiliones, salvage logging, spiders, topography, wind disturbance

Introduction

Large wind disturbances are important drivers of forest ecosystem dynamics (Thorn *et al.* 2017b). In the last decades, European conifer forests have experienced several extreme events causing massive forest losses (Seidl *et al.* 2020). After these events, to save timber yield and to prevent bark beetle outbreaks, salvage logging has been often carried out as a common post-event management strategy (Marini *et al.* 2022). During dead wood removal operations, salvage logging alters soil and microclimate, often increasing soil compaction and erosion with potential negative effects on biodiversity (Thorn *et al.* 2018). Several forest-related taxa might be impacted by these environmental changes and, in particular, ground-dwelling organisms are expected to be sensitive due to their reduced mobility (Buddle *et al.* 2000, Bouget and Duelli 2004, Thorn, Bußler, *et al.* 2016). Since extreme events are expected to increase in terms of magnitude and frequency in the future (Seidl *et al.* 2020), understanding how forest communities respond to these abrupt ecological changes is pivotal for addressing conservation and management actions.

Previous ecological studies have often compared different post-event management strategies or quantified differences between disturbed and undisturbed forests (Phillips *et al.* 2006, Kašák *et al.* 2017, Wermelinger *et al.* 2017b, Elek *et al.* 2018). However, the effects of both large-scale disturbances and salvage logging on biodiversity can be also modulated by underlying ecological gradients of pre-disturbance conditions. In mountain regions, topography is expected to be particularly important to modify the effect of canopy removal. First, disturbed forests at high elevations are expected to exhibit slower vegetation recovery due to colder temperatures and to be exposed to more extreme climatic conditions. Second, soils on steep slopes should be more sensitive to superficial erosion, landslides and high insolation.

To evaluate the role of elevation, slope, and aspect in modifying the compounded effect of wind disturbance and salvage logging on ground-dwelling organisms, we used a multi-taxa approach sampling spiders, ground beetles, and harvestmen. These groups were selected because they exhibit different mobility, habitat specialization and hunting strategies (Gerlach *et al.* 2013). After disturbance, community assembly dynamics should critically depend on species dispersal (Gravel *et al.* 2006). On the one hand, recolonization events based on short-range movement are dependent on cursorial activity and capacity of crossing habitat boundaries (Jopp and Reuter 2005). On the other hand, long-distance dispersal such as ballooning in spiders might be important for facilitating rapid colonization of isolated disturbed patches by open-habitat species

(Entling et al., 2011). As dispersal can be predicted based on species traits, trait-based analyses can help to better understand species responses to forest disturbances (Carvalho and Cardoso 2014, Pedley and Dolman 2014).

Here, we aimed at quantifying the short-term response of harvestmen, ground beetles, and spiders to the compounded effect of wind disturbance and salvage logging along steep topographical gradients in spruce conifer forests impacted by the storm "Vaia" in NE Italy. We investigated alpha, beta and functional diversity of ground beetles, harvestmen and spiders by comparing disturbed vs. un-disturbed areas along statistically independent gradients in elevation, slope, and aspect. Specifically, we aimed to address the following ecological questions: (i) Does the effect of wind disturbance on diversity depend on topography? (ii) Are there specific taxon-related responses to disturbances?, and (iii) What is the role of dispersal in shaping species assembly dynamics?

Materials and Methods

Study area and sampling design

The sampling was carried out in the Province of Trento, NE Italy (11.70° E 46.32° N – 11.88° E 46.20° N, WGS 84), within the protected area Paneveggio-Pale di S. Martino. The study area was severely hit by Vaia windstorm in October 2018 (Chirici *et al.* 2019). By photointerpretation of high-resolution satellite images based on NDVI Sentinel 2 layer, we polygonised windthrow areas for site selection. We selected 11 landscapes (radius 500 m) ranging from 1100 to 1800 a.s.l. (Fig. 1), including both remnant intact forest patches and windthrow gaps. To remove all fallen trees, forestry operations have been carried out in 2019 in all selected landscapes. Due to the lack of sites without salvage logging (control), it was not possible to include this treatment in our study. Hence, we could only evaluate the compounded effect of wind disturbance and salvage logging and we were not able to disentangle the effects of the single factors.

Landscapes were chosen to avoid collinearity among the selected environmental variables: slope, elevation, aspect (i.e. distance from south direction in degrees) (Appendix A). In each landscape, we selected five sampling points in windthrow gaps and five in the closest intact forests following a systematic grid. Within each landscape, average minimum distance among sampling locations was c. 75 m. For each sampling location, we extracted elevation, aspect (i.e. distance from south direction), and slope from a digital elevation model with a 1 m spatial resolution (http://www.territorio.provincia.tn.it).

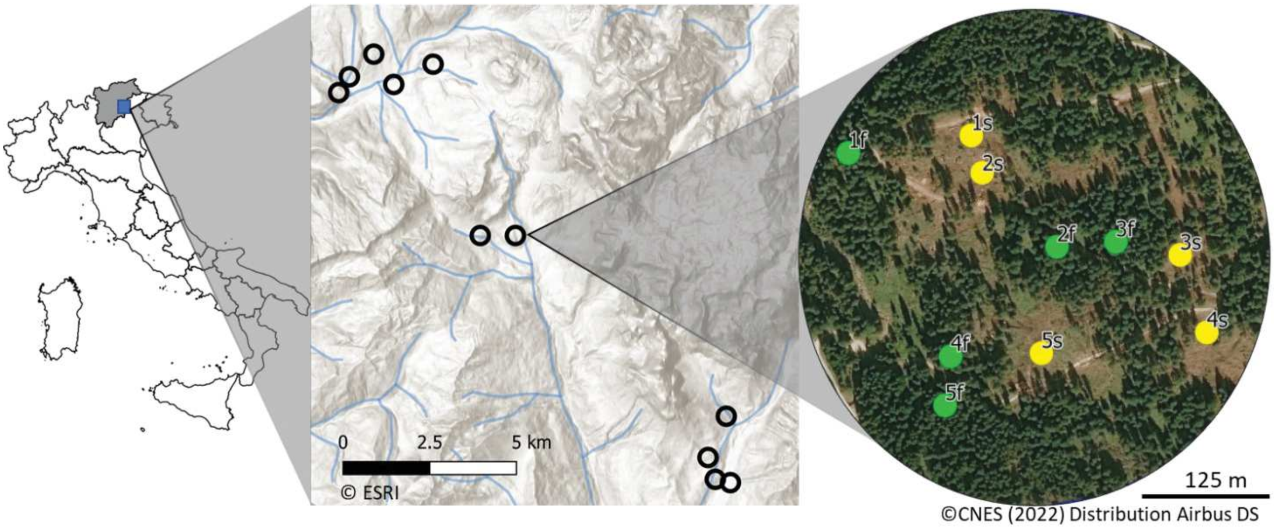

Figure 1 - Sampling was carried out in Trentino (Italy) within the natural park "Parco Paneveggio - Pale di San Martino". Eleven landscapes (black circles) were chosen in wind-damaged areas to obtain statically orthogonal gradients in elevation, slope, and aspect. Within each habitat type, 10 sampling points, consisting of two pitfall traps, were placed and equally distributed among two habitat types: intact forest (green dots) and windfalls (yellow dots).

Arthropod sampling

For each sampling point, we placed two pitfall traps c. 10 m apart. Each pitfall trap consisted of a 0.5 L plastic cup (diameter of 10 cm, depth of 14 cm) buried in the soil and covered by a plastic plate. A metal wire cage (mesh size 1 cm) was placed between soil surface and plastic plate (approximately 10 cm height) to reduce small vertebrate by-catching. Pitfalls were activated with 75% propylene glycol and a drop of detergent. Ground-dwelling arthropods were sampled in June and July 2020, with 2 rounds of 14 days each. After field collection, arthropods were stored in ethanol for lab sorting. We sampled only two rounds due to the short growing season. We determined adult specimens of spiders and ground beetles to species level, while sub-adult spiders were pooled at species, genus, or subgenus level, if possible, otherwise they were discarded from analyses. Spider and ground beetle nomenclature were updated following the World Spider Catalog (2021) and Fauna Europea database (www.fauna-eu.org) respectively. Harvestmen were sorted to morphospecies and then determined to genus level following key by Chemini (1984). Community data were pooled at sampling point level by merging captures from the two traps.

Temperature measurements and remote sensing assessment

To measure temperature changes, 30 dataloggers were used in five landscapes covering the elevational range of sampling (for each landscape we placed three dataloggers in both forests and windfalls). Dataloggers were buried at about 5 cm and recorded temperature every 5 minutes. Finally, to remotely assess vegetation recovery rate, July average-NDVI map was computed in Google Earth Engine using free available Sentinel 2 data, and mean values of NDVI were extracted from windfall polygons for each landscape.

Statistical analyses

Alpha diversity

For each taxon, we computed species richness and activity density. To test if species richness and activity density were affected by habitat type (i.e. intact forest and windthrow areas), topography (slope, elevation, aspect) and their interaction, we ran mixed-effect models. For activity density, we used a generalized mixed model with a negative binomial distribution with the following formula:

Activity density ~ elevation * habitat type + slope * habitat type + aspect * habitat type.

Landscape identity was used as random effect. We did not directly use temperature and NDVI mean value for windfalls in the models as they exhibited a strong correlation with elevation. For species richness, we used linear mixed-effect models testing the same fixed effects as in the activity density model and landscape identity was used as random effect. Statistical analyses were done in R (R Core Team 2022) using VEGAN (Oksanen *et al.* 2020), EFFECTS (Fox and Weisberg 2019), LME4 (Bates *et al.* 2015) packages. DHARMA (Harting 2021) package was used for residuals diagnostic.

Beta-diversity

To visualize the spatial community dissimilarity of species composition, we ran NMDS on abundance-based data by using Chao index (Chao *et al.* 2005). To test the effects of habitat type on community composition we used a partial-RDA analysis controlling for the effect of landscape identity. Community data were transformed using the Hellinger transformation. Significance of habitat type was tested using a Montecarlo permutation test with 999 permutations.

In addition, to quantify the components of community dissimilarity between intact forests and windfalls, we used presence/absence data to compute the replacement and the nestedness components of beta dissimilarity (Cardoso *et al.* 2009, Podani and Schmera 2011, Schmera *et al.* 2022). Within each landscape, we created five pairs of forest-windfalls samples. We paired neighboring sampling points belonging to different habitat types based on their minimum distance. Then, for each pair we computed neutral turnover (i.e., replacement) and the directional gaining nestedness components on a presence/absence matrix using adespatial (Dray *et al.* 2022). The gaining nestedness was computed from forest to windfall to test if post-disturbance communities (i.e., windfall) are subsets of the initial conditions (i.e., intact forest). The indices were relativized using Jaccard denominator to make them independent from species richness. We ran linear mixed-effect models using taxon as fixed effect and trap pair nested into landscape as random factor. Differences in replacement and nestedness among taxa were assessed by post-hoc Tukey test. Statistical analyses were done in R (R Core Team 2022) using vegan (Oksanen *et al.* 2020), effects (Fox and Weisberg 2019), lme4 (Bates *et al.* 2015) packages. DHARMa (Harting 2021) package was used for residuals diagnostic.

Dispersal trait analysis

Finally, we wanted to test if community changes after windstorm were influenced by dispersal strategies. For spiders, ballooning propensity of each species was retrieved from https://spidertraits.sci.muni.cz/ (Pekár *et al.* 2021) and coded as a binary variable (value 1: high propensity; value 0: low propensity). Fifteen species (about 3% of collected spider specimens) were discarded from the analysis because information on ballooning propensity was not available. For ground beetles, we used wing morphology as a proxy for long-range dispersal by defining macropteran species, in which wings are present in at least one sex and brachypteran species, in which wings are not present. For each species, wing morphology was retrieved from the literature (Casale *et al.* 1982, Freude *et al.* 2004, Brandmayr *et al.* 2005) and coded as binary variable (value 1: macropterans; value 0: brachypterans). Harvestmen were not considered because they lack any long-range dispersal ability. All traps belonging to the same habitat type were pooled at the site level and then community weighted means of dispersal traits were calculated for each taxon. Finally, linear mixed-effect models were used to compare communities sampled in forests vs. windfalls.

Results

General and alpha diversity results

We collected 4353 (31 species) ground beetles, 5368 (116 species) spiders, and 3477 (13 morphospecies) harvestmen (further details in Appendix C). Regarding activity density, interactions between elevation and slope and habitat type were observed for all taxa (Fig. 2). Ground beetles showed an increasing activity density in forests and a decreasing activity density in windfalls with increasing elevation (habitat x elevation, P=0.04) (Fig. 2 A). We found no significant effect of slope on ground beetle density. Spiders showed an opposite pattern (Fig. 2 B): in windfalls abundance increased with elevation while in forests we observed a negative effect of elevation (elevation x habitat type: P<0.001). Harvestman activity density increased in forests and decreased in windfalls along the elevation gradient (habitat x elevation, P<0.001). Overall, lower activity density was observed in windfalls (Anova test for interaction habitat type: P<0.001) (Fig. 2 C). In windfalls, activity density of harvestmen decreased with increasing slope (Anova test for interaction slope x habitat type: P = 0.002) (Fig. 2 D).

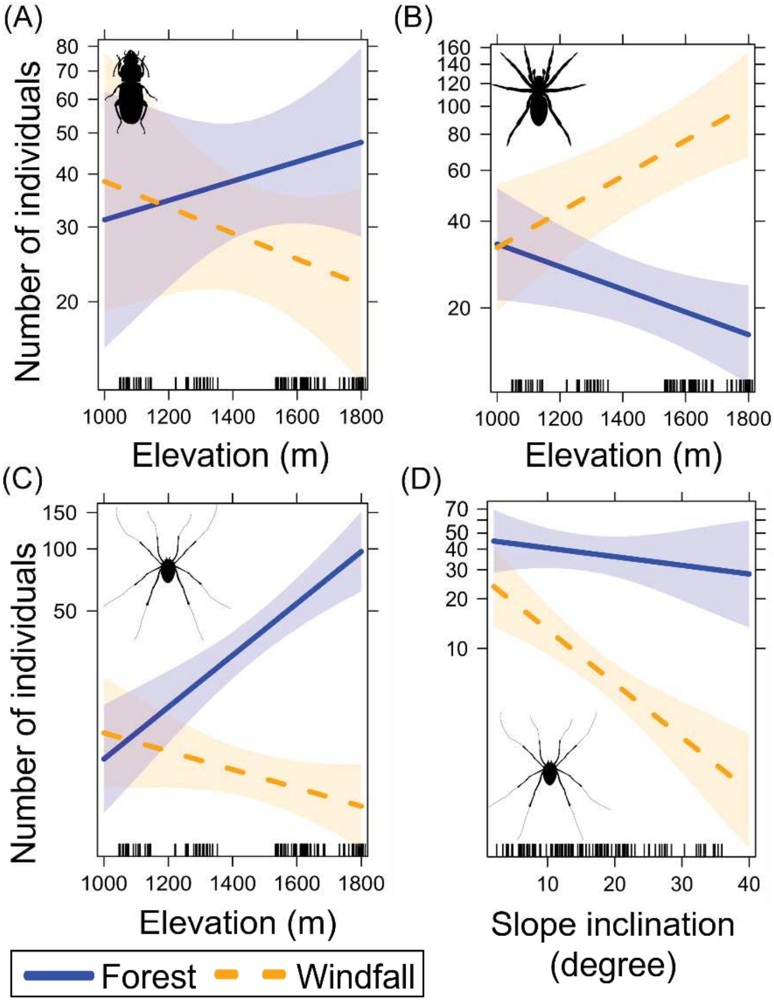

Figure 2 - Activity density of ground beetles (Fig. 2A), spiders (Fig. 2B) and harvestmen (Fig. 2C-D) varied along elevation and slope. Only significant interactions between elevation/slope and habitat type (i.e. forest and windfall) are shown. We used mixed-effect models to test the effects of habitat type, elevation, slope, and aspect on the activity density, using a random effect for controlling for landscape identity. A negative binomial distribution was used to meet model assumptions.

For species richness, we did not find any difference between habitat types for ground beetles (Fig. 3 A). For spiders, species richness was higher in windfalls than in forest (Anova test for habitat type, P<0.001), while an opposite trend was observed for harvestmen (Anova test for habitat type, P=0.008). Finally, we did not find significant effects of aspect (i.e. slope facing) for either activity density or species richness in any group.

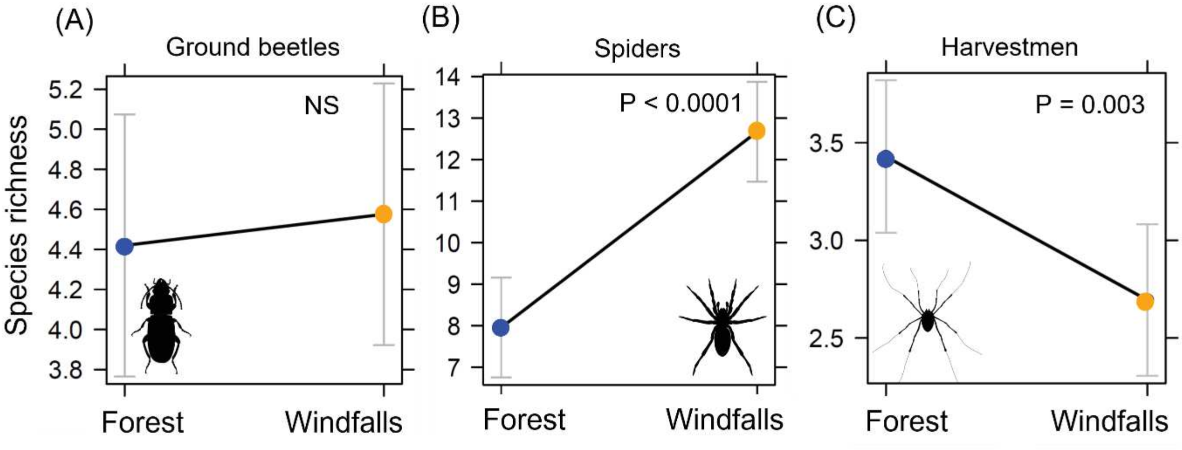

Figure 3 - Species richness of ground beetles (Fig. 3A), spiders (Fig. 3B) and harvestmen (Fig. 3C) in two habitat types (forest and windfalls). Ground beetles showed no effect of wind disturbance, while spider species richness increased in windfalls and harvestmen species richness decreased in windfalls. We used mixed-effect models to test the effects of habitat type, elevation, slope, and aspect on the species richness, using a random effect for controlling for landscape identity.

Beta-diversity analyses

NMDS and partial-RDA analyses revealed that forest and windfall communities were differently structured between taxa (Fig. 4). In particular, for ground beetles habitat type (i.e., disturbance effect) had a low explanatory power in partial-RDA analysis ($P = 0.001$, $R^2 = 0.03$). Instead, for spiders and harvestmen a larger effect of habitat type was found, also showing two clear clusters in NMDS (spiders: $P = 0.001$, $R^2 = 0.12$; harvestmen: $P = 0.001$, $R^2 = 0.13$).

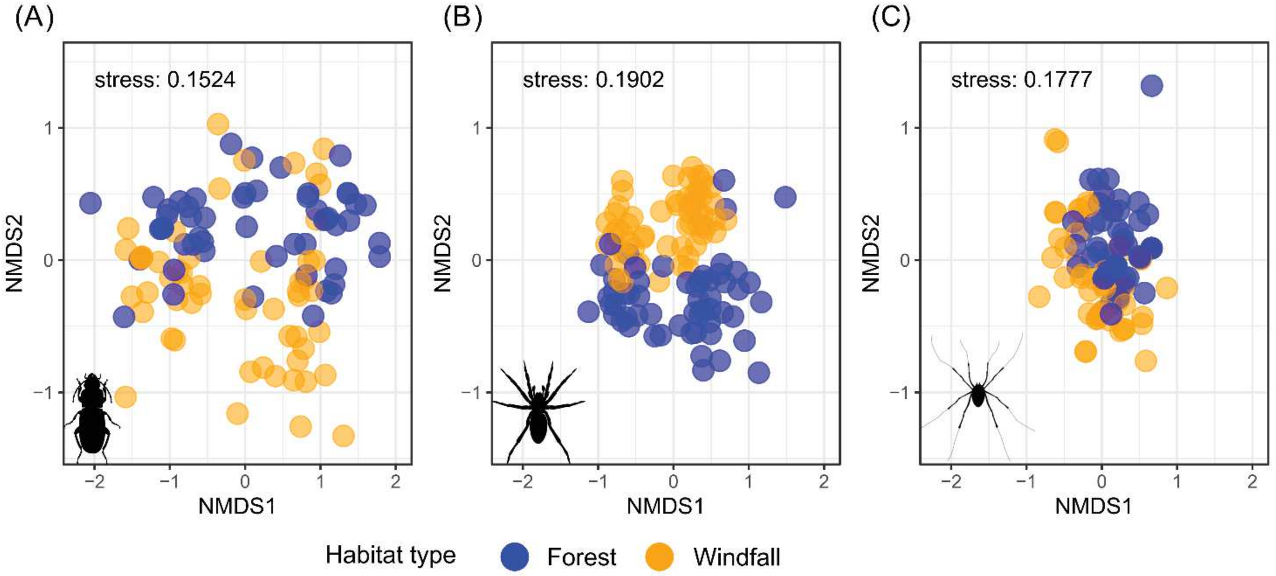

Figure 4 - For ground beetles (Fig. 4(A), spiders (Fig. 4B) and harvestmen (Fig. 4C) NMDS ordinations of communities belonging to intact forest (blue dots) and windfalls (orange dots) were computed based on the Chao dissimilarity index (abundance data).

We investigated the neutral replacement and the directional nestedness components of the beta dissimilarity in species assemblages from forest to windfall, showing that each taxa had different pattern (Fig. 5). In particular, species replacement in spiders showed higher values than in ground beetles and harvestmen (spiders: 0.46, ground beetles = 0.27, harvestmen = 0.29; Tukey test for pairwise comparison: spiders – ground beetles $P \leq 0.001$; spiders – harvestmen $P < 0.001$; ground beetles – harvestmen $P = 0.866$) (Fig. 5A). In contrast, ground beetles showed higher values of the gaining nestedness from forest to windfall (spiders: 0.44, ground beetles = 0.61, harvestmen = 0.49; Tukey test for pairwise comparison: spiders – ground beetles $P = 0.003$; spiders – harvestmen $P = 0.573$, ground beetle – harvestmen $P = 0.049$) (Fig. 5B).

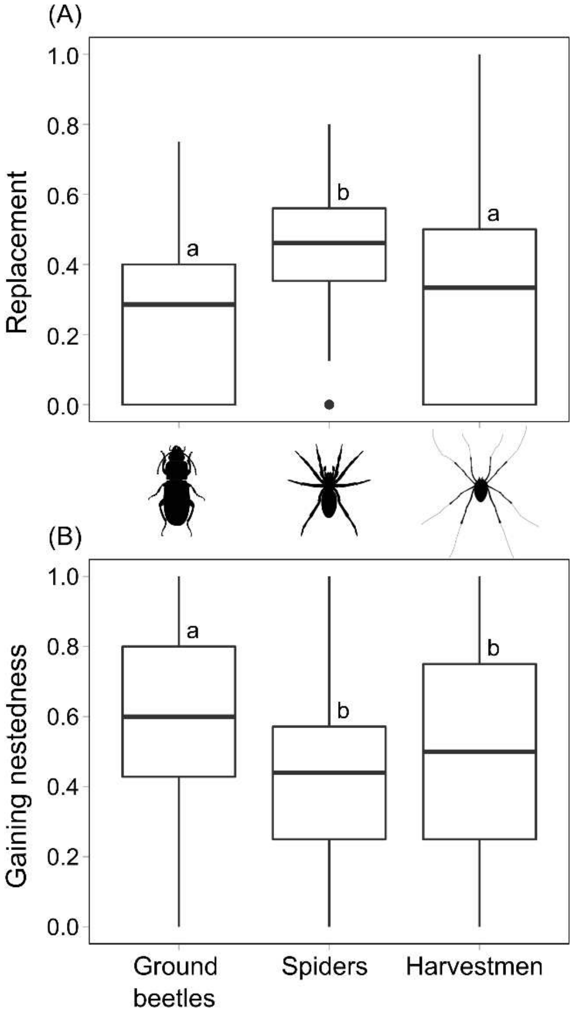

Figure 5 - For each taxon, we showed neutral replacement (Fig. 5A) and gaining nestedness (Fig. 5B) between neighboring forest-windfall communities. Letters indicate significant differences in the post-hoc test, and refer to linear mixed-effect models. Indices were computed on presence/absence data and relativized with Jaccard denominator.

Dispersal strategy

In our study, windstorm disturbance affected functional composition of communities belonging to the two different habitats (Fig. 6). Windfall communities hosted more species with long dispersal strategy, i.e. ballooners for spiders and macropteran species for ground beetles (P value for ground beetles = 0.008; P value for spiders = 0.0001).

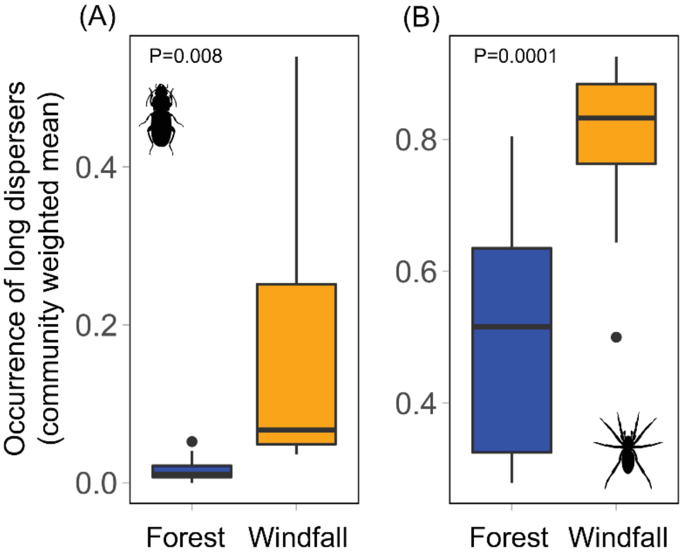

Figure 6 - For ground beetles (Fig. 6A) and spiders (Fig. 6B), we computed community weighted mean of dispersal strategies (binary variable: 1 for long dispersers, 0 for short dispersers). The response variable varies between 0, i.e. communities including only short-range dispersers, and 1, i.e. communities including only long-range dispersers. Statistical assessment was performed with linear mixed-effect models for testing differences between habitats.

Discussion

Our observational study quantified the short-term response to wind disturbance of ground-dwelling communities in temperate forest ecosystems. Although several studies investigated the effect of forest disturbance (natural disturbance or forest management) on ground-dwelling communities (e.g. Elek et al., 2018; Phillips et al., 2006; Thorn et al., 2016), here we tested for the first time the interaction between forest disturbances and topography, showing that, in mountain areas, slope and elevation strongly modulate the combined effect of wind disturbance and salvage logging on ground beetles, spiders, and harvestmen.

Interaction between local disturbance and underlying environmental gradients

For ground beetles, activity density was higher in forests than in windfalls, as already observed in previous studies (Kašák *et al.* 2017). In windfalls, abiotic changes, such as increased temperature, higher solar radiation and lower moisture might contribute to this pattern, since forest ground beetles avoid more variable microclimatic conditions typical of open habitats (Thiele 1977). Moreover, we found that activity density increased with increasing elevation in forests, but decreased in windfalls. At high elevations the difference in temperature between windfalls and forest was larger and the vegetation recovery was slower than at low elevations (Appendix B). Hence, the higher ecological contrast after one year from salvage logging might play an important role in increasing the impact of local disturbance (see below).

For spiders, we found a contrasting pattern, i.e. windfalls hosted higher species richness and activity density than forests. Previous studies found similar results pointing out the importance of canopy openings in promoting spider diversity at the landscape scale (Nardi and Marini 2021). In particular, at high elevations, windfalls hosted high abundance of running wolf spiders belonging to the genus *Pardosa* (e.g. *Pardosa ferruginea*), which commonly occur in disturbed habitats (Larrivée *et al.* 2008, Pinzon *et al.* 2012). Differences between forests and windfalls also increased at high elevations, suggesting that similarly to ground beetle, habitat contrast at high elevation might lead to a greater impact of disturbance.

For harvestmen, we found that activity density and species richness were higher in forests than windfalls. We further observed a decrease of harvestmen activity density on steep slopes. Studies on canopy effect showed similar results for activity density between forest and open habitats such as grasslands and clear-cuts (Kataja-aho *et al.* 2016, De Smedt *et al.* 2019, Stašiov *et al.* 2021). Moreover, harvestmen, especially forest species, are usually sensitive to low moisture, thus decreasing under dry conditions (Novak *et al.* 2017). Finally, harvestmen can disperse only by actively moving on the ground or vegetation, resulting in a low mobility (Giribet and Kury 2007). Hence, observed patterns may be due to the combination of restricted microclimatic preferences and low mobility.

Generally, our findings suggest that the effect of wind disturbance was greater at high elevations, where we found stronger shifts in species composition. Indeed, high elevation habitats host communities with cold-adapted species and might be severely threatened by environmental changes as warned by several long-term studies (Pizzolotto *et al.* 2014). Studies on plant communities already showed that sites located at high elevations experienced a greater shift to thermophilic communities after windstorm, compared to lowland sites (Dietz *et al.* 2020). However, disentangling the pure elevation effect from other factors is difficult because other environmental gradients often covary with elevation. For instance, despite the well-known gradient of temperature along elevation, we found that vegetation biomass, remotely assessed as NDVI index, was higher in windfalls at low elevation sites (Appendix B, Fig. B.2), probably because of a longer growing season. Changes in vegetation composition and structure may also affect arthropod succession, leading to a stronger effect of disturbance where a higher contrast of environmental conditions exists (Schaffers *et al.* 2008, Malumbres-Olarte *et al.* 2013). These interactive effects of local disturbance and topography should be considered by forest managers to address restoration and conservation goals after disturbance, especially in protected areas.

Taxon-specific response of faunal succession after disturbance

For ground beetles, the large overlap in composition between forest and windfall communities suggests a persistence of a subset of forest species also in windfall areas. Accordingly, persistence of zoophagous and brachypterous forest species in the early stage of succession after windstorm has already been observed (Skłodowski 2017). Here, we showed that communities occurring in forest and windfall habitats are slightly different and many species are still shared between forest and disturbed sites. Because ground beetles are active walkers and often habitat generalists (Lami *et al.* 2021), a larger overlap between forest and windfall assemblages was expected. The high values of directional nestedness indicated that most of the species occurring in forest habitat were still present after disturbance. This supports the hypothesis of a higher plasticity of ground beetles or, alternatively, a slower response to disturbance. As other studies showed a dramatic changes in species composition also in the short term (Gandhi *et al.* 2008), these contrasting findings may suggest that community changes might also be related to other factors, such as site characteristics, dispersal strategy, or different temporal scales (Kašák *et al.* 2017).

On the contrary, spiders and harvestmen showed a higher turnover in species composition between forest and windfall. In particular, spider communities occurring in forest and windfall sites were clearly different, suggesting a high divergence of species assemblages between these two habitats, even if sampling points were located at very short distance. Vegetation structure might affect spider species assemblages because of changes in moisture, light, and shelter availability (Entling et al., 2007; Oxbrough et al., 2010; Schaffers et al., 2008; Ziesche & Roth, 2008). Although both spiders and ground beetles are active walkers, spiders usually show a stronger habitat specialization and rarely occur outside their optimal habitat (Michalko *et al.* 2016, Nardi *et al.* 2019, Nardi and Marini 2021). For spiders, our findings supported the hypothesis of a high sensitivity of forest species to disturbance. The high species replacement and the low nestedness from forest sites to windfall sites indicated that spider communities after disturbance are characterized by a strong turnover in species composition with a significant loss of forest species. Similarly, in a previous study investigating post-fire disturbance ground beetles showed lower recovery rate and more simplified communities than spiders (Samu *et al.* 2010).

The role of dispersal

Different dispersal strategies might affect the capacity of colonization of novel habitats by arthropods (Moir *et al.* 2005). In particular, we found that the proportion of short- and long-range dispersal species of ground beetles and spiders changed between forest communities and windfall communities. Indeed, our windfalls hosted more species possessing long-range dispersal strategies than forests for both ground beetles and spiders (Fig. 6), suggesting that species with long-range dispersal ability replaced poor dispersers in the new forest openings. Long-range dispersers are facilitated in colonizing newly created habitats because of higher probability of reaching new patches far from source habitats, especially for disturbed habitats (Entling et al., 2011). Similar findings have already been reported in agricultural ecosystems. For instance, macropterous species of ground beetles are less sensitive to isolation, than brachypterous species (Fischer *et al.* 2013).

Conclusions

Our study showed that the local impact of forest disturbance changed along steep gradients in elevation and slope. Ground-dwelling arthropod communities inhabiting high elevation windfalls showed more marked differences in terms of activity density and species richness compared to the neighboring intact forests. However, understanding the underlying mechanisms is difficult because many putative drivers such as climate and vegetation recovery might be involved and responses may vary among different taxa. Responses to disturbance varied also depending on dispersal strategy. Forest managers should be aware that wind disturbances, and consequent salvage logging, may have different effects on forest ecosystems depending on elevation and slope of the impacted forests. For these reasons, different restoration actions should be considered in order to preserve forest ground-dwelling arthropods and facilitate the establishment of new communities in disturbed patches.

Acknowledgements

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CHAPTER II

Impact of forest disturbance on microarthropod communities depends on underlying ecological gradients and species traits

Davide Nardi, Diego Fontaneto, Matteo Girardi,
Cristiano Vernesi

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Abstract

Windstorms and salvage logging lead to huge soil disturbance in alpine spruce forests, potentially affecting soil-living arthropods. Impacts on soil microarthropods are poorly studied, particularly interactions with underlying ecological gradients. Here we used a DNA-metabarcoding approach to study wind-induced disturbances on forest communities of springtails and soil mites. We aimed to test the effect of forest soil disturbance on abundance, richness, species composition, and functional guilds.

We sampled 29 pairs of windfall-forest sites across gradients of elevation, precipitation, aspect and slope, two years after a massive windstorm, named Vaia, which hit North-Eastern Italy in October 2018. As general outcome, wind-induced disturbances led to detrimental impacts on soil-living communities. Abundance of microarthropods decreased in windfalls, but with interacting effects with precipitation gradients. Richness strongly decreased after disturbance too, particularly with a reduction in species belonging to plant-related trophic guilds. Furthermore, species composition analyses revealed that communities occurring in post-disturbance plot were different than those in intact forests. However, variables at different spatial scales played different roles depending on the considered taxon.

Our study contributes to shed light on important but often neglected arthropod communities after windstorm in spruce forests. Effects of forest disturbance are mediated by underlying large scale ecological gradients, such as precipitation and topography, as well as micro-scale factors. Massive impacts of stronger and more frequent windstorms might hit forests in the future; given the response we recorded, mediated by environmental features, forest managers need to take site-specific conservation measures.

Keywords (5): mites, springtails, windstorm, trophic guild, precipitation

Introduction

Windstorms are natural disturbances that have periodically occurred in Europe, shaping the structure of forests (Ulanova 2000). However, due to climate change, windstorms are expected to increase in frequency and magnitude, causing tree uprooting at large spatial scale and damaging timber production (Seidl et al. 2014). Wind and other natural forest disturbances, such as fire, heavy snowfall, and pests, are well-known to increase landscape heterogeneity and to promote habitat succession and climate adaptation (Attiwill 1994, Dietz et al. 2020). Furthermore, such disturbances usually benefit forest biodiversity by increasing niche availability and diversity at landscape scale (Bouget and Duelli 2004). However, after windstorm, fallen trees are usually logged, according to current regulations in many countries, to prevent subsequent tree mortality, mainly due to bark beetles infestations (Leverkus et al. 2021). Unfortunately, salvage logging causes additional disturbance on forest ecosystem leading to negative effects on soil communities because of machinery activities, removal of dead wood, and changes in soil exposure (Thorn *et al.* 2017a, 2018, Rousseau *et al.* 2019). For these reasons, forecasting general outcomes on the effect of windstorm in forest is challenging because the response of biological communities also depends on post-disturbance management and taxon-specific characteristics. Moreover, because of the large spatial extent, extreme events might lead to interactions between forest disturbance and underlying ecological gradients, such as topography, forest types, and climatic gradients, thus showing a non-linear response of forest communities (Foster *et al.* 1998, Abedi *et al.* 2022, Nardi, Giannone, *et al.* 2022).

Commonly studied groups, such as pollinators, ground-dwelling arthropods, dead-wood beetles, and vertebrates, respond positively to canopy openness after wind disturbance (Bouget and Duelli 2004, Bouget 2005, Thorn, Werner, et al. 2016). However, soil is a poorly studied system and very little is known about responses of soil-living communities (Decaëns 2010). Previous studies demonstrated that soil disturbances might affect a wide range of soil-living arthropods in temperate forest (Blasi et al. 2013). Springtails and soil mites are amongst the most important groups within soil ecosystems, playing a pivotal role in providing ecosystem services such as organic matter decomposition, nutrient recycling, and food webs (Seastedt 1984). Moreover, soil-living communities are known to strongly respond after changes in habitat characteristics, such as nitrogen addition, temperature, elevation (Hågvar and Klanderud 2009, Mitchell et al. 2016, Bokhorst et al. 2018), and canopy openness (Perry et al. 2018). Despite previous studies have investigated the effects of wind and salvage logging on soil microarthropod communities (e.g. Kokořova and Starý 2017, Čuchta et al. 2019), the potential interactions of underlying environmental on diversity, including functional guilds, is still poorly understood.

Here, we aimed to study the effect of windstorms on forest soil using soil-inhabiting mites (mainly Mesostigmata and Oribatida) and springtails (Collembola) as model groups. We used eDNA metabarcoding to partially overcome the difficult morphological species identification of forest microarthropods and reveal dark taxa (Sire et al. 2022). We attempt to understand the ecological outcomes of the forest habitat changing after windstorm and the subsequent salvage logging on microarthropod communities. In particular, we are interested in highlighting interactive effects with underlying ecological gradients. We investigated the response of springtails and soil mites using abundance (individual counting), richness (from DNA-based identifications), trophic guilds, and species composition.

Materials and Methods

Sampling design and site selection

Sampling was carried out within the Eastern Italian Alps, between Trento and Vicenza provinces. Our study area was severely hit by Vaia windstorm in October 2018 causing large damages (Chirici et al. 2019). Windthrows mainly occurred on spruce forests and with a patchy distribution. Within our study area, windfalls were firstly mapped with high-resolution satellite images. A Digital Elevation Model (DEM, 25 m resolution) was retrieved from www.land.copernicus.eu and was used to compute topography-related variables, i.e. elevation, slope (inclination degree), aspect (radiant distance from South). Data from 61 local climate stations were used to obtain mean annual precipitation using kriging interpolation methods in SAGA version 7.8.2 (Conrad et al. 2015). For each station, climatic data series of the previous 10 years were retrieved from www.meteotrentino.it and www.arpav.it. We selected 29 sites, from four geographic zones, according to independent gradients of elevation, precipitation, slope, and aspect (Figure 1). Field site inspections were carried out to assess operator accessibility, salvage logging operations, and the presence of undisturbed intact forest nearby. Only sites with a clear predominance of Norway spruce (*Picea abies* (L.) H. Karst.) forests and already logged windfalls were considered eligible.

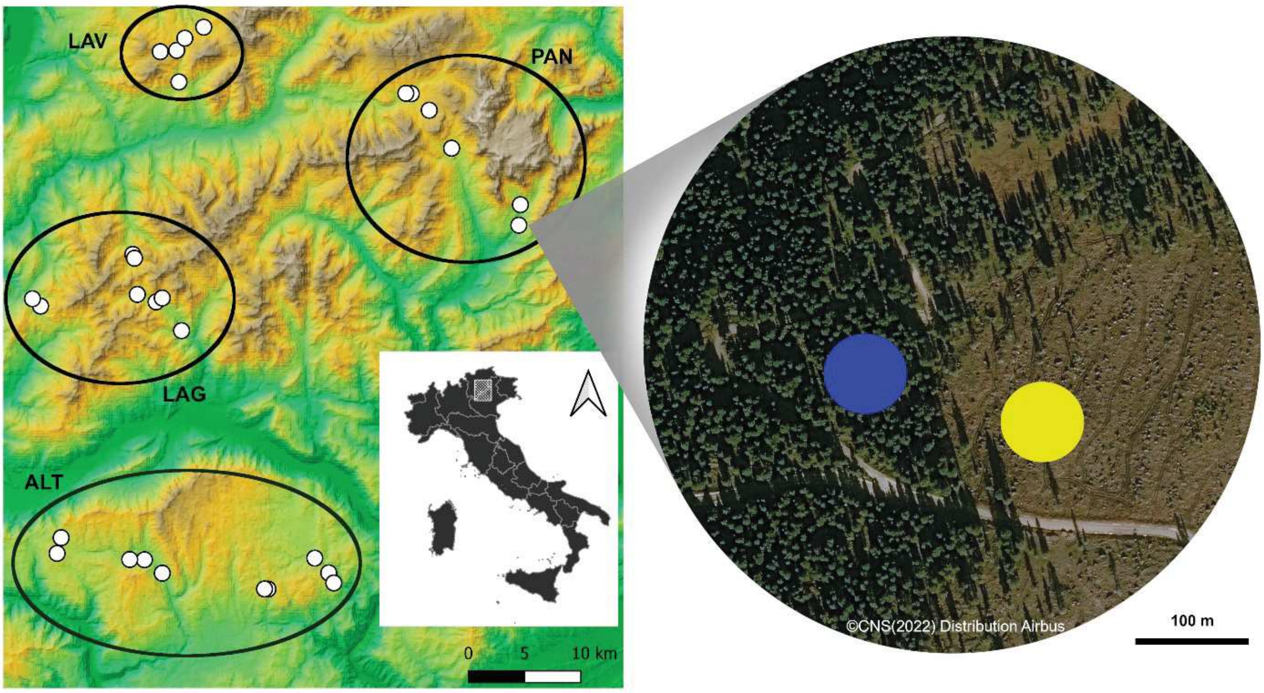

Figure 1 - Sampling design consisted in 29 pair sites (white circles on the left image) of windfall (yellow circle on the right image) and intact forest (blue circle) across different ecological gradients. The four geographic zones in the left image are highlighted with black ellipses: Lavazé (LAV), Paneveggio-Pale di San Martino (PAN), Western Lagorai (LAG), and Altopiano di Asiago (ALT).

Once in the field, for each selected site, we choose two sampling points following a pair-based sampling design, by including a windfall area and an undisturbed forest area with similar topographic conditions. We kept a minimum distance of about 30 m from boundaries and ecotones to avoid edge effects. Geographic positions of each sampling point were recorded with a GPS receiver. Given the precise location of each sampling point, elevation, slope, and aspect were computed again. The average distance within pairs was 114 m. Within each sampling point, we selected 3 pseudo-replicated small plots of 20 x 20 cm. In windfall habitat, bare soil due to uprooting and machinery trails was avoided, and samples were taken from undamaged soil. For each pseudo-replicate, surface moss vegetation and soil until 5 cm depth were collected using a shovel. Percentage of moss cover was recorded by visual inspection estimates (Supplementary B). For each sampling point, the three pseudo-replicates were mixed and pooled in a unique sample before extraction of invertebrates. Tools used for soil collection were cleaned before changing sampling point using bleach solution. We performed two rounds of sampling during 2020, in June and in September. A sample of sieved soil (c. 10 g) was preserved from the last round for organic matter, hereafter OM, analysis.

Sample preparation and DNA sequencing

In the laboratory we extracted arthropods from about 4 L of soil for each sampling site using a Berlese apparatus maintained active for three weeks. Animals were collected in propylene glycol and then were stored in absolute ethanol. For each sample we retained only those invertebrates that were morphologically recognized as belonging to soil mites (orders Sarcoptiformes, Trombidiformes, and Mesostigmata) or springtails (class Collembola) using decontaminated forceps and small brush. Abundances of mites and springtails were counted under a dissecting microscope, as the number of individuals cannot be retrieved from DNA metabarcoding results. All animals from each site, collected during the first and second round of sampling, were pooled together and stored in absolute ethanol until DNA extraction. Before DNA extraction, samples were dried in a vacuum centrifugal machinery to remove ethanol. During counting and dehydration steps, some microcentrifuge tubes were left open to check for potential contamination (negative controls). DNA extraction was performed using DNeasy® PowerMax® Soil extraction kit (Qiagen, Hilden, Germany). DNA extractions of negative controls were routinely processed to assess contaminants from the lab procedure. We amplified a 313-base pair (bp) fragment of the mitochondrial DNA Cytochrome oxidase c subunit I (COI) gene. PCR amplification was done using the mlCOIintF forward primer 5′-GGWACWGGWTGAACWGTWTAYCCYCC-3′ and jgHCO2198 reverse primer 5′-TAIACYTCIGGRTGICCRAARAAYCA-3′ (Leray *et al.* 2013). Prior to PCR amplification, a PCR condition setting up was performed to optimize amplicon yield. 5 µL of DNA was added to 45 µL of PCR mix, including 23.75 µL of water, 10 µL of FlexiBuffer, 6 µL of MgCl solution (25 mM), 2 µL of each primer (10 ρmol/µL), 1 µL of dNTPs (10 mM), and 0.25 µL of Promega GoTaq Hot Start G2 (Promega, Madison, WI, USA). PCRs were run under the following conditions: one preincubation step of 95 °C for 2 min, followed by 45 cycles of 95 °C for 30 s, 47 °C for 60 s and 72 °C for 60 s, with a final extension at 72 °C for 5 min. All DNA amplifications were performed in a Veriti 96-Well Fast Thermal Cycler (AB Applied Biosystems).

For each sample three PCR replicates were performed, and the resulting amplicons were pooled before the purification step. Purification was carried out using QIAquick PCR purification kit (Qiagen, Hilden, Germany). Amplifications of negative controls belonging to the same PCR run were pooled. Short-read Illumina amplicon sequencing (300 bp) was performed at IGA Technology Services, using an Illumina NOVASEQ6000.

Bioinformatic pipeline

Demultiplexed paired-end raw reads were used to retrieve ASVs (Amplicon Sequence Variants) using a custom pipeline. First, primers were cut using CUTADAPT (Martin 2011) and reads without primers were discarded. Second, we used a denoising approach to retrieve Amplicon Sequence Variants (ASVs). Reads were filtered, denoised, merged, and chimeras were removed using DADA2 version 1.16 package (Callahan *et al.* 2016).

We performed a first taxonomic assignment of ASVs using Bayesian classifier in QIIME2 (https://qiime2.org) and BLASTN on a custom database. Unassigned, low confident (< 0.97 for Bayesian confidence or < 0.97 identity for BLASTN) or ambiguous ASVs were mapped against BOLD database to confirm their identity. ASVs that were successfully assigned to our target groups (i.e. class Collembola and orders Sarcoptiformes, Mesostigmata, and Trombidiformes) were retained, whereas those not belonging to these groups were discarded. A further curation step was performed to remove sequences with gaps or stop codons, since the amplicon region was expected to be entirely coding.

Approaches combining denoising and clustering generally produce reliable species-like entities, which are relatively similar to those obtained with non-molecular approaches (Antich *et al.* 2021). However, different taxa might show different barcoding gap size, by varying intra- and inter-specific distance. Commonly used clustering algorithms (such as VSEARCH and SWARM) depend on *a priori* settings and they were not optimized for a relaxed taxonomic clustering. Thus, we used an approach from DNA taxonomy, namely ASAP (Puillandre *et al.* 2021), developed to identify the most appropriate distance threshold for species-level clustering from alignments of DNA sequences. ASAP clustering was performed separately for the ASVs of each group, soil mites and springtails. To increase the reliability of the approach, we downloaded all available species-level COI sequences of mites and springtails from BOLD database, aligned and trimmed them to our ASV datasets, and use the large alignments in ASAP (https://bioinfo.mnhn.fr/abi/public/asap/). Following ASAP, ASVs were merged into Operative Taxonomic Units (OTUs). Each OTU was identified at the best taxonomic resolution according to ASV taxonomic assignment, and eventually updated according to ASAP clustering results. The final OTUs table was also reduced by removing OTUs with read numbers accounting for less than 0.1 % in each sample, to further diminish the risk of false positives in our DNA metabarcoding pipeline. The resulting OTU table was used as the base for the following ecological analyses (Supplementary A).

Hypothesis testing

First, we tested the effect of Vaia windstorm on the overall abundance of microarthropods obtained from visual counts. We used linear mixed-effect models (LMMs) with habitat type (two levels: windfall and undisturbed forest) as a predictor, in addition to elevation, precipitation, slope, aspect, OM, and their interaction with habitat type as fixed effects, with the identity of each pair of samples nested in geographic zone (four levels) as random effect. Non-significant interaction terms were removed, and models were run again. LMMs were fitted using LME4 package version 1.27.1 (Bates *et al.* 2015) in R version 4.1.3 (R Core Team 2022). The response variable was log-transformed to meet model assumptions. We used DHARMA version 0.4.5 (Harting 2021) and CAR version 3.0 (Fox and Weisberg 2019) packages for checking model assumptions and collinearity among predictors. Analysis-of-variance tables were extracted with function *Anova*() in CAR.

Second, we investigated the effect of Vaia windstorm on species (OTU) richness. The models we used had the same structure and rationale of the LMMs used for abundances, separately for each of the two taxonomic groups.

Third, we investigate the effect of disturbance on functional guilds, assigning each OTU to trophic niches based on literature. Soil mites were divided in predators (including omnivorous) and no predators (including primary and secondary decomposers). We preferred using broad categorization since the trophic guilds of many species were unknown (literature review was based on Schneider *et al.* 2004, Maraun *et al.* 2011, Fischer *et al.* 2014, Maaß *et al.* 2015, Schaefer and Caruso 2019, Nae *et al.* 2021). Springtails were divided following Potapov *et al.* (2016) in two ipogeic guilds (i.e. euedaphic end hemiedaphic) and in two epigeic guilds (i.e. animal consumers and plant consumers). To test the effect of disturbance on trophic guild we used LMMs with number of OTUs as response variable; trophic guild, habitat, and interaction between trophic guild and habitat type as predictors; site ID nested in pair ID nested in geographic area as random factor. The response variable was log-transformed for soil mite dataset. We used DHARMA and CAR packages as for the other models; in addition, pairwise comparisons were extracted with EMMEANS package (Lenth *et al.* 2020).

Fourth, we investigate differences in species composition (i.e. beta diversity) due to disturbance. To test the effect of ecological predictors on species composition we used Adonis analysis using VEGAN version 2.7 (Oksanen *et al.* 2020). As a response variable, we used occurrence-based Sorensen beta dissimilarity index among communities of springtails and soil mites, separately. As predictors, we used habitat type, slope, mean annual precipitation, aspect, elevation, and OM, with geographic zone and pair ID as blocks. We used 9999 permutations for P value calculation.

Results

Overall, we counted 15800 soil mites (average number in each sample = 272) and 7270 springtails specimens (average number in each sample = 125). After sequencing and demultiplexing the mean number of raw reads per sample was 29588 reads ± 7293 SD (minimum = 10544, maximum = 44896). After DADA2 pipeline, we retrieved a mean number of 16770 ± 4723 SD reads per sample, constituting in total 3041 ASVs (Amplicon Sequence Variants). However, only 1518 ASVs belonged to our target groups, which were aggregated to 441 total OTUs (289 belonging to mites, and 152 belonging to springtails) using ASAP clustering step (further details in Appendix A). Both pre-PCR negative controls (extraction and sorting blanks) and PCR blanks did not contain amplified DNA.

Regarding abundance data, we found that windfalls hosted overall fewer individuals than forest sites for both soil mites and springtails (Figure 2, Table 1). However, we observed that disturbance effect depends also on underlying abiotic factors. Indeed, we found significant interactions of habitat type with annual precipitation for mites. We observed larger effect size (i.e. decreasing abundance in windfalls) in those sites with low mean annual precipitation.

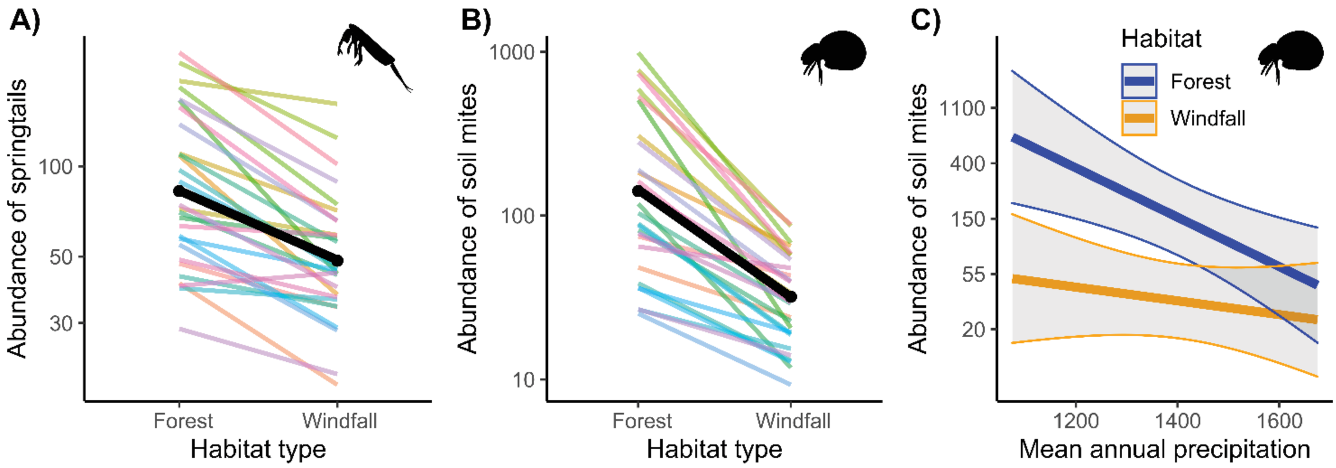

Figure 2 – The effects of habitat type on the abundance of springtails (Fig. 2 A) and mites (Fig. 2 B) are shown: the overall effect is shown in black, random component (pair ID) in colour lines. Interactions between habitat type (intact forest in blue, windfalls in orange) and the mean annual precipitation on soil mites' abundance are shown (Fig. 2 C).

Table 1 - Anova-table results of abundance-based models for mites and springtails, with F and P values. Number of asterisks refer to significance levels: * = P < 0.05, *** = P < 0.001.

Soil mites			
	F	P	
Windfall	30.11	< 0.0001	***
Precipitation	3.30	0.1140	
Precipitation:Habitat	6.01	0.0210	*
Elevation	2.96	0.0978	
Slope	0.52	0.4739	
Aspect	2.81	0.1016	
OM	0.31	0.5814	
Springtails			
	F	P	
Windfall	5.55	0.0254	*
Precipitation	5.20	0.0754	
Elevation	0.84	0.3689	
Slope	1.11	0.2987	
Aspect	2.05	0.1598	
OM	1.80	0.1856	

Similarly to abundance data, OTU richness decreased significantly after soil disturbance for both groups, soil mites and springtails (Fig. 3, Table 2). Although we did not find significant interactions with underlying gradients, we found that richness was still shaped by ecological gradients. Soil mite richness decreased with precipitation and aspect, whereas springtail richness decreased along elevation (Table 2).

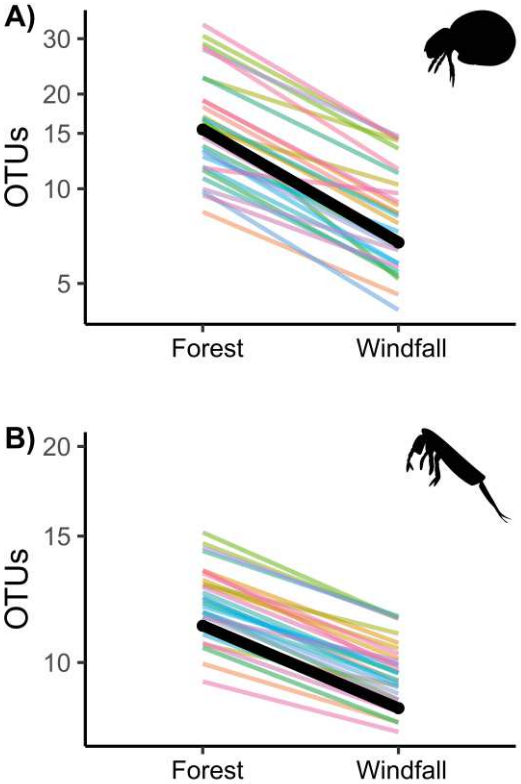

Figure 3 – OTU richness of soil mites (Fig. 3 A) and springtails (Fig. 3 B) compared between forest and windfalls samples. The overall effect is shown in black, random component (pair ID) in colour lines.

Table 2 - Anova-table results of OTU richness model for mites and springtails, with F and P values. Number of asterisks refer to significance levels: * = P < 0.05, ** = P < 0.01, *** = P < 0.001.

Soil mites			
	F	P	
Windfall	15.28	0.00053	***
Annual precipitation	7.52	0.01115	*
Elevation	3.21	0.08581	
Slope	3.10	0.08754	
Aspect	4.21	0.04782	*
OM	0.66	0.42145	
Springtails			
	F	P	
Windfall	10.27	0.00334	**
Annual precipitation	1.98	0.17186	
Elevation	4.56	0.04289	*
Slope	2.65	0.11288	
Aspect	0.38	0.54328	
OM	0.23	0.63615	

The effects of soil disturbance on trophic guilds of soil mites and springtails showed different responses. Separately for each group, we assessed the response of OTU richness for each trophic guild in interaction with habitat type. In soil mites, we found that both predators and no-predators decreased in windfalls (habitat type, P < 0.001) without interactions between trophic guild and habitat type (P = 0.66). On the contrary, in springtails we found that soil disturbance affected epigeic plant consumer guild more than the other trophic guilds (Fig. 4, Table 3).

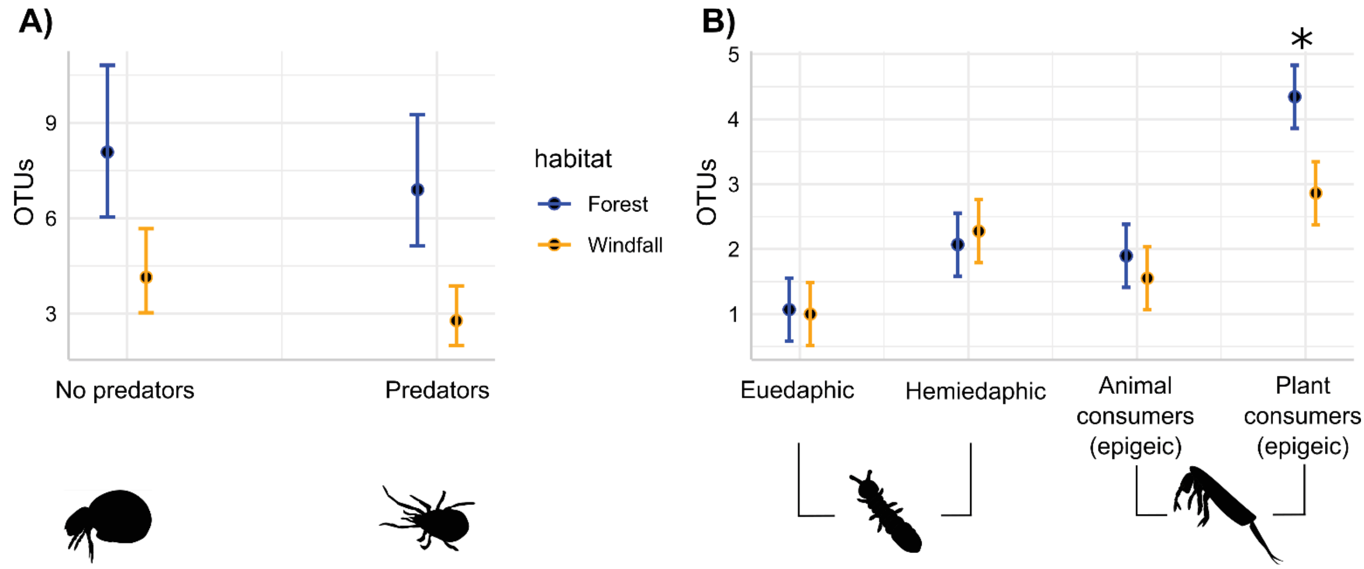

Figure 4 - Soil disturbance effect on trophic guilds. For soil mites (Fig. 4 A) and for springtails (Fig. 4 B), the number of OTUs belonging to each trophic guild is compared across the two different habitats: intact forest (blue) and windfall (orange).

Table 3 - Pairwise comparisons between forest and windfall for each trophic guild of springtails. Estimates and Standard Errors (SE), t, and p values are reported.

Trophic guild	Habitat contrast	Estimate	SE	t	P
Euedaphic	forest-windfall	0.14	0.35	0.39	0.6940
Hemiedaphic	forest-windfall	-0.21	0.35	-0.59	0.5552
Animal consumers (epigeic)	forest-windfall	0.31	0.35	0.89	0.3765
Plant consumers (epigeic)	forest-windfall	1.41	0.35	4.04	0.0001

Finally, we investigated beta diversity patterns to compare communities in intact forest and windfalls (Fig. 5). Soil mites showed a higher dissimilarity among samples (mean = 0.90, SD = 0.10) than springtails (mean = 0.81, SD = 0.13). We found that habitat type (i.e. forest – windfall) and OM are key-variables for species composition in both investigated groups (Table 4). Also, geographic zone greatly contributed to explaining species composition for springtails ($R^2 = 0.12$, P value = 0.01). Despite we found important factors explaining differences in beta diversity among samples, a large part of variance remained unexplained by the models (77% for mites and 63% for springtails).

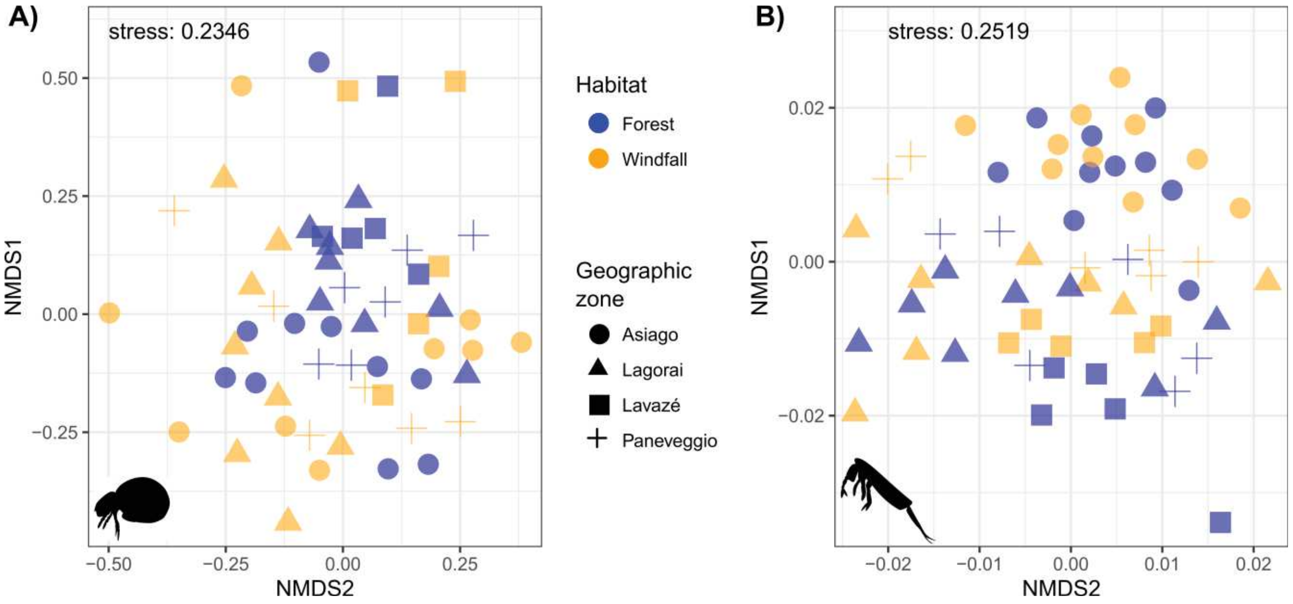

Figure 5 - NMDS based on presence-absence dissimilarity index for soil mites (Fig. 5 A) and springtails (Fig. 5 B). Habitat type is shown by colour (blue = forest; orange = windfall), geographic zones are shown by shapes (dot = Altopiano di Asiago; triangle = Lagorai; square = Lavazé; plus = Paneveggio-Pale di San Martino).

Table 4 - Results of Adonis model for mites and springtails. Degrees of freedom (DF), R2, F, and P values are reported.

Soil mites					
	DF	R^2	F	P	
Wind disturbance	1	0.0264	1.62	0.0170	*
Geographic zone	3	0.0581	1.19	0.4751	
Elevation	1	0.0271	1.66	0.6514	
Annual precipitation	1	0.0259	1.59	0.3897	
Aspect	1	0.0192	1.17	0.2845	
Slope	1	0.0187	1.14	0.6955	
OM	1	0.0216	1.32	0.0284	*
Springtails					
	DF	R^2	F	P	
Wind disturbance	1	0.0339	2.59	0.0001	***
Geographic zone	3	0.1209	3.08	0.0107	*
Elevation	1	0.0297	2.27	0.0734	
Annual precipitation	1	0.0291	2.22	0.2756	
Aspect	1	0.0164	1.25	0.0315	*
Slope	1	0.0210	1.60	0.558	
OM	1	0.0200	1.53	0.0360	*

Discussion

After a massive windstorm disturbance, communities of microarthropods were investigated in intact forests and windfalls using eDNA metabarcoding. We assessed springtails and soil mites over large spatial scale to test interactions between wind disturbance and underlying ecological gradients. Beside the overall decreasing abundance and species richness in post-disturbance communities, we found that windstorm effect is mediated by ecological gradients and taxa characteristics. Topography and climatic conditions can mediate the effect of windstorm-induced disturbance, with different taxonomic groups showing contrasting responses.

Effects of wind-induced disturbance at larger spatial scale

Our results showed an overall and strong decline of microarthropod abundance and richness in windfalls, compared to near intact forest sites (Fig. 2 – 3). Similarly, previous studies showed negative effects of windstorm and salvage logging on communities of springtails (e.g. Čuchta *et al.* 2019, Sławski and Sławska 2019), soil mites (Lóšková *et al.* 2013, Wehner, Simons, *et al.* 2021), and proturans (e.g. Sterzyńska *et al.* 2020). These studies suggested that soil perturbations could strongly modify microarthropod communities and, thus, their ecological functioning. Biomass and diversity of microarthropod communities are important factors that can affect decomposition processes and microbial fauna (Marshall 2000). Declining pattern safter disturbance were mainly associated with a decrease of resources and habitat suitability. For instance, soil perturbations, such as salvage logging, negatively affected wood-inhabiting fungi and mosses (Thorn *et al.* 2018), thus contributing to a decrease in available resources for microarthropods (Rousseau *et al.* 2019). Generally, specialist species strongly decreased in abundance and diversity after disturbance in forest, and post-disturbance communities are mainly constituted by few high-adaptable species, such as *Tectocepheus* sp. and some species belonging to Entomobrydae (Maraun *et al.* 2003). In the case of oribatid mites, post-disturbance communities are often dominated by species with disturbance adaptations, such as parthenogenetic reproduction (Wehner, Schuster, *et al.* 2021). However, other studies found that richness of collembola increased in disturbed plot (Urbanovičová *et al.* 2010, 2014), and others found divergent responses in abundance and species richness (Čuchta *et al.* 2012). On the one hand, these differences might depend on the time span of the studies since the response may change depending on time from disturbance (Čuchta *et al.* 2019). Previous studies on microarthropod after intense drought indicated that mites are slower than springtails in recovery process (Lindberg and Bengtsson 2005). On the other hand, different responses might depend on other interacting factors.

We showed that interaction between canopy openness (i.e. wind-induced disturbance) and precipitation influenced the response of soil communities to disturbance. We found higher effect size of disturbance on mite abundance at low mean annual precipitation (Fig. 2). In other words, drier conditions (i.e. low annual precipitations and steep slopes) showed higher loss of mite individuals after forest canopy removal. Changing in drier conditions might have negative effects on microarthropod communities since litter moisture is known to be an important factor for microarthropods (Hopkin 1997, Lindberg and Bengtsson 2005). Indeed, precipitation gradient can strongly influence soil biota, especially for forest ecosystems where aridity might have detrimental effects on living-communities (Blankinship *et al.* 2011). Recently, it has been shown that underlying ecological gradient, such as elevation and slope, can play a role in determining differences in the response of communities after a large-scale disturbance (Foster *et al.* 1998, Abedi *et al.* 2022, Nardi, Giannone, *et al.* 2022). Therefore, we suggest that disturbance-driven soil impacts might exacerbate under climate change in the future, especially for forest ecosystems. Despite soil disturbance after windstorms could be intensified by topography conditions, such as steep slopes, due to soil instability (Mitchell 2013), we did not find interactions with other local factors. Probably our large-scale approach cannot effectively catch effects at smaller spatial scale.

Effects on trophic guilds

Microarthropods could exhibit a large differentiation in trophic niche and feeding preferences, even within taxonomic groups, such as oribatid mites (Schneider *et al.* 2004) and springtails (Potapov *et al.* 2016). However, after disturbance, ecosystems could exhibit trophic web declining with collapsing of certain trophic niches. For instance, oribatid communities in plantations showed missing niches in food webs compared to rainforest habitat (Krause *et al.* 2021), and springtails seem to compensate the decreasing interspecific niche partitioning with wider intraspecific feeding preferences in disturbed habitat (Korotkevich *et al.* 2018). Here, we assessed the effect of soil disturbances on trophic guilds to test whether forest disturbances can influence functional traits in the disturbed soils. We found that functional guilds of soil mites and springtails are differently affected by windstorm. In particular, we observed that the richness of soil mites strongly declined regardless of trophic guilds. Previous studies found that the proportion of detritivore oribatid mites might depend on forest management (Farská *et al.* 2014). Many reasons could be advocate for explaining the lack of this effect in our data. First, trophic guild assignment was based on taxonomies, since we could not directly measure it. Since taxa might be assigned with different taxonomic resolution, those with low taxonomic resolution cannot be specifically addressed to precise trophic niche, but we used general trophic niche (mostly at family level). Second, we used a coarse trophic partitioning, to include taxa with wide range of trophic preferences (generalists or poor-studied taxa). Moreover, previous studies showed that the same species can slightly change its feeding preferences under certain environmental conditions (Melguizo-Ruiz *et al.* 2017, Maraun *et al.* 2020). Specific approach, such as isotopic analyses might provide further insights on the effect of soil food webs after wind disturbances in temperate forests (Maraun *et al.* 2011).

On the contrary, we found significant interactions between habitat type and trophic guild in springtails. Here, we found that plant-related consumers were the most affected guild in windfalls. In fact, moss cover dramatically decreased in windfalls due to higher insolation (Appendix B), and salvage logging might largely contribute by exacerbating the desiccation process (Waldron *et al.* 2014). Our results agreed with previous studies emphasizing that specialist and bryophilous species of springtails are the most sensitive ones to environmental changes after forest clearings (Urbanovičová *et al.* 2013). Actually, the combining effect of canopy openings and salvage logging led to huge changes in superficial soil litter, vegetation, and moss cover (Rumbaitis del Rio 2006), largely affecting species related to litter microhabitats, in particular specialists. Despite our studies focused on short-term effects, similar long-term studies revealed that springtail communities can remain affected by the disturbance even for decades (Sławski and Sławska 2019). Hence, we suggest that our findings on springtail perturbations in windfall communities might persist might have long-term outcomes. Here, we showed that mite and springtail communities might have different response to soil disturbance: overall decreasing for soil mites and guild-related loss for springtails.

Effects of soil disturbance on species composition

In our analyses soil mites and springtails responded to different spatial scales. These results agreed with literature, suggesting that dispersal might contribute in post-disturbance communities with group-related responses (Rousseau *et al.* 2019). Soil mites exhibited a high dissimilarity among samples, suggesting that the processes producing species assemblages may occur at small spatial scale and a high diversity exists in forest communities (Fig 5). Our results showed that habitat type and OM are the most important factors contributing to differences in species composition, thus suggesting that windfall and intact forest host completely different communities and differences in mite communities occurred at very small scale. On the contrary, geographic area did not play an important role in the model. Moreover, our model revealed a relatively high amount of unexplained variance, probably due to the high diversity and dependence of microscale conditions. Our findings agreed with the low mobility and high environmental niche preferences of this group (Lehmitz *et al.* 2012). Thus, even short distances may actually reflect huge differences in terms of environmental variables, as similar studies found that soil mite communities can differ within few metres (Dong *et al.* 2017).

Much more similar communities are expected in springtails since they have higher mobility than mites, especially those species with a well-developed furca (Potapov *et al.* 2020). Indeed, in our model the main factor shaping differences between communities was geographic zone, while habitat type, aspect, and OM were less important (Fig. 5). Our findings suggested that geographic distance had a higher explanatory power than soil disturbance on differences in species assemblages in springtails. Our result might depend on two main reasons. First, besides the relevance of microenvironmental parameters, within continuous habitat types springtail communities might be shaped by geographic distance due to their limiting dispersal (Arribas *et al.* 2021). Second, the higher explanatory power of geographic distance than habitat type might still reflect a short-term response to disturbance. Here we sampled pure spruce forests (i.e. a single forest type) just after two years from disturbance, thus it is not surprising that geographic zone (i.e. related to historical patterns) is still the most important factor. On the other hand, small-scale variables, such as habitat type, still play a great importance as predictors for species composition, in agreement with previous studies (Salmon and Ponge 2012, Sterzyńska and Skłodowski 2018, Arribas *et al.* 2021).

Conclusions

Our results suggested that windstorm-induced disturbance might have detrimental effects on soil microarthropods in temperate forests, at least in the short term. Negative effects on soil functionality and diversity could affect bio-mediated soil processes such as decomposition (Marshall 2000). Furthermore, changes in habitat vegetation and soil decomposer communities may have bottom-up effects, also affecting upper trophic guilds, such as predatory macroinvertebrates (Laigle *et al.* 2021). Natural disturbances are extremely complex phenomena and interactions between wind-induced disturbance and other large-scale or micro-scale underlying ecological gradients might reduce or increase the effect on arthropod soil communities. Hence, since increasing soil disturbance in forests, as well as drying climate, are expected in the near future, conservation actions and mitigation measures should be prioritized by forest management after natural disturbances. Finally, we showed how DNA metabarcoding could be used as an integrative approach, to help identify and monitor taxonomic groups that are poorly known but highly ecologically relevant in forest ecosystems.

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CHAPTER III

Unrevealing oomycete communities' dynamics after windstorm disturbance in alpine Norway spruce forests: a metabarcoding approach

Davide Nardi, Duccio Migliorini, Cristiano Vernesi, Alberto Santini

Abstract

Understanding the outcomes of a massive windstorm disturbance on soil communities of plant pathogens is of pivotal importance for forest management. Oomycete communities host some species of plant pathogens, which might affect the regeneration after the disturbance. Here, we carried out a large sampling to compare three habitats (i.e., windfall, old clearings, and intact spruce forest) along a gradient of elevation and slope. We used an environmental DNA metabarcoding approach targeting the mitochondrial rps10 gene. Our results showed that both wind disturbance and underlying topography can influence the richness of oomycete ASVs. Disturbed sites exhibited a higher richness of oomycetes compared to the intact forest. Also, we found a positive correlation with steepness. Regarding community composition, oomycetes are patchy distributed at the landscape level, without differences among the different habitat types. On the contrary, we found significant differences at the scale of the drainage basin. Our work contributed to the understanding of the oomycete communities in the natural Norway spruce forest and the effect of wind-related disturbances in forest.

Keywords (5): oomycetes, metabarcoding, windstorm, topography, rsp10

Introduction

Windstorm disturbance can lead to heavy environmental changes in temperate forests. Canopy removal due to tree uprooting drives subsequential changes concerning direct insolation, soil temperature, and soil chemical (Mitchell 2013). Furthermore, salvage logging is often carried out in wind-damaged managed forests to prevent bark beetle infestations (Leverkus *et al.* 2018, Thorn *et al.* 2018, Kleinman *et al.* 2019). A large body of literature agrees on the negative effect of salvage logging, because strongly affecting soil communities due to dead wood removal and machinery compaction (Lindenmayer and Noss 2006). Soil perturbations due to salvage logging might change microbial communities and thus facilitating non-native and pathogenic organisms (García-Carmona *et al.* 2021). Indeed, forest disturbances could actually modify the incidence of forest diseases by changing host availability or by limiting/increasing the spread of pathogens (Giordana *et al.* 2020, Simler-Williamson *et al.* 2021).

One of the most important groups of soil pathogens is the group of oomycetes. Oomycetes are eukaryotic micro-organisms, which are globally distributed and well adapted to a large variety of environments (Thines 2014). Many species are tree pathogens, e.g. Pythiaceae family, and they might play an important role in disturbed forests, possibly affecting forest regeneration in the medium-long term (Domínguez-Begines *et al.* 2020, 2021). However, the functional role of this group in the forest soil ecosystems is still poor-studied, and only few genera have been extensively investigated, such as *Pythium* and *Phytophthora*. The soilborne oomycete genus *Pythium* is mainly pathogenic on forest seedlings as damping off agent (Agrios 2005, Beakes and Thines 2016), but some species might have different trophic strategies in the absence of plant host and their life forms can persist in the soil, thus playing an important role in litter degradation (Kramer *et al.* 2016). On the contrary, *Phytophthora* genus has attracted significantly more interest and some of its most aggressive species were exhaustively studied in the past (Burgess *et al.* 2017). Indeed, *Phytophthora* genus includes numerous species that can strongly compromise the host physiology in all its growth stages, from seedling to adult plant (Hansen 2015) and the knowledge gained about the genus *Phytophthora* represents therefore the unique case study of oomycetes main ecological traits in forest ecosystems. Besides the high importance of oomycetes communities in the agroecosystems, where their presence and influence are of a primary concern (Agrios 2005), their landscape-scale occurrence in natural habitats is still little known. Despite a few case studies have revealed that oomycete communities are correlated with the environmental factors such as altitude, geomorphology and soil structure (Sapp *et al.* 2019), limiting factors and dispersal distance are poor understood factors in oomycete communities. Moreover, distance decay among communities has been rarely investigated at large scale for these organisms (Sapp *et al.* 2019).

A hierarchy of abiotic and biotic soil characteristics were found to directly and indirectly affect disease occurrence due to *Phytophthora* genus (Shearer and Hill 1989, Shearer 2014). The most important abiotic factors are water presence, temperature, and soil properties (Erwin *et al.* 1983, Vettraino *et al.* 2005), whereas soil microbiota is a relevant biotic factor (Malajczuk *et al.* 1983). The importance of water in oomycete dispersal has been largely observed by the rapid progress of the disease front during the outbreak of singular *Phytophthora* species along roads and recreational trails where zoospores active transport occurs via subsurface water after rain events (Davidson *et al.* 2005, Hardy *et al.* 2007). The amount of water in the soils can also influence the sporangia production (Duniway 1975, Gisi 1980). Thus, field experiments showed that soil properties can directly influence *Phytophthora* sp. development and spreading (Marks and Kassaby 1972, Podger 1972, Kliejunas 1976, Marks and Smith 1981, Moreira and Martins 2005, Shearer and Crane 2011).

Moreover, soil microbiota affects the fluctuation dynamic of *Phytophthora* sp. by influencing the more viable forms, i.e. hyphae, sporangia, and motile zoospores (Malajczuk *et al.* 1983). The presence of soil bacteria and fungi was found to have significant effects on the induced microbiota antagonistic control of *Phytophthora* soil spread (Dixon *et al.* 1989, Blaya *et al.* 2016, Bonanomi *et al.* 2018).

The occurrence of soilborne plant pathogens in natural habitats has been traditionally assessed with baiting protocols until the past decade (Erwin and Ribeiro 1996, Jung *et al.* 2016, 2018). However, the recent greater availability of High-Throughput Sequencing techniques (HTS) allow researchers to use environmental-DNA approach (eDNA) for rapid and large-scale surveys of soil pathogens (Riddell *et al.* 2019, Fiore-Donno and Bonkowski 2021). The use of eDNA has some advantages comparing to previous techniques, such as carrying large scale sampling surveys and studying the whole community in soil regardless their active pathogenicity. For these reasons, eDNA approach has been implemented in many field investigations in the last years (Prigigallo *et al.* 2015, Burgess *et al.* 2017, Bose *et al.* 2018, Khaliq *et al.* 2018, Redondo *et al.* 2018).

At the end of October 2018, a windstorm called “Vaia” occurred in NE Italy, severely hitting the Italian alpine region and uprooting about 40,000 ha of Norway spruce forest (Giannetti *et al.* 2021). Due to the highspeed wind gusts reached during the storm, many windthrow gaps have been created by changing the mountain landscape. The most damaged forests were secondary and natural forests of Norway spruce. Since oomycetes can remain in the soil without expressing pathogenicity, soil samples can host different quiescent communities of possible pathogens. In particular, damping-off agents, such as the oomycete genera *Pythium* and *Phytophthora,* may be responsible for pre- and post-emergent seedling mortality in restoration planting (Lamichhane *et al.* 2017). For these reasons e-DNA approach is an appropriate tool for better understanding the role of soil oomycetes after forest disturbances and their implications for forest regeneration. Here, we aimed to firstly investigate potential soil pathogen communities in a poor studied environment, such as alpine coniferous forests, and to understand the effects of wind disturbance on the diversity of oomycete communities. In particular, we are interested in studying the compound effects of soil alteration, topography, and geography on the occurrence of soil-living oomycetes in semi-natural forests.

Materials and Methods

Sampling design

The sampling was carried out in the Province of Trento, NE Italy (11.70° E 46.32° N – 11.88° E 46.20° N, WGS 84), within Paneveggio-Pale di S. Martino protected area. During October 2018 a windstorm occurred in our study area, severely damaging Norway spruce forests (Chirici *et al.* 2019). We selected 10 sites (areas with 500 m radius) ranging from 1100 to 1800 m a.s.l. in three different valleys: Val Canali (4 sites), San Martino di Castrozza (2 sites), Paneveggio (4 sites). Unfortunately, the reduced number of sites in San Martino basin was due to low availability of accessible windthrow areas. More details on sampling areas are summarized in Table 1.

Valley	**Study sites**	**Altitude (m a.s.l.)**	**Rainfall (mm)**	**Temperature (°C)**	**Substrate**	**Forest type**
Val Canali	4	1100-1400	1690	7.7	Carbonate bedrock	Secondary Norway spruce forests mixed with silver fir
San Martino di Castrozza	2	1500-1700	1560	5.4	Volcanic bedrocks	Seminatural Norway spruce forests
Paneveggio	4	1500-1800	1619	2.8	Glacial deposits of both carbonate and volcanic origins	Seminatural Norway spruce forests

Table 1. Main characteristics of the sampling areas. Rainfall = Mean annual total rainfall; Temperature = mean annual temperature.

The three valleys represents distinctive hydrological drainage basins according to superficial topography and analyses in SAGA version 7.8.2 (Conrad *et al.* 2015). Sites were chosen to cover different environmental conditions of slope and elevation. In each site, we selected nine sampling points including three points in windthrow gaps, three in intact forests and three in pre-existing clearings. Pre-existing clearings, i.e. old clearcuts, natural openings or ecotones, were characterized by no spruce tree canopy cover, flourishing herbaceous stratum, and presence of shrubs or young trees. For each sampling point, we extracted elevation and slope inclination from a digital elevation model with a 1 m of spatial resolution (http://www.territorio.provincia.tn.it).

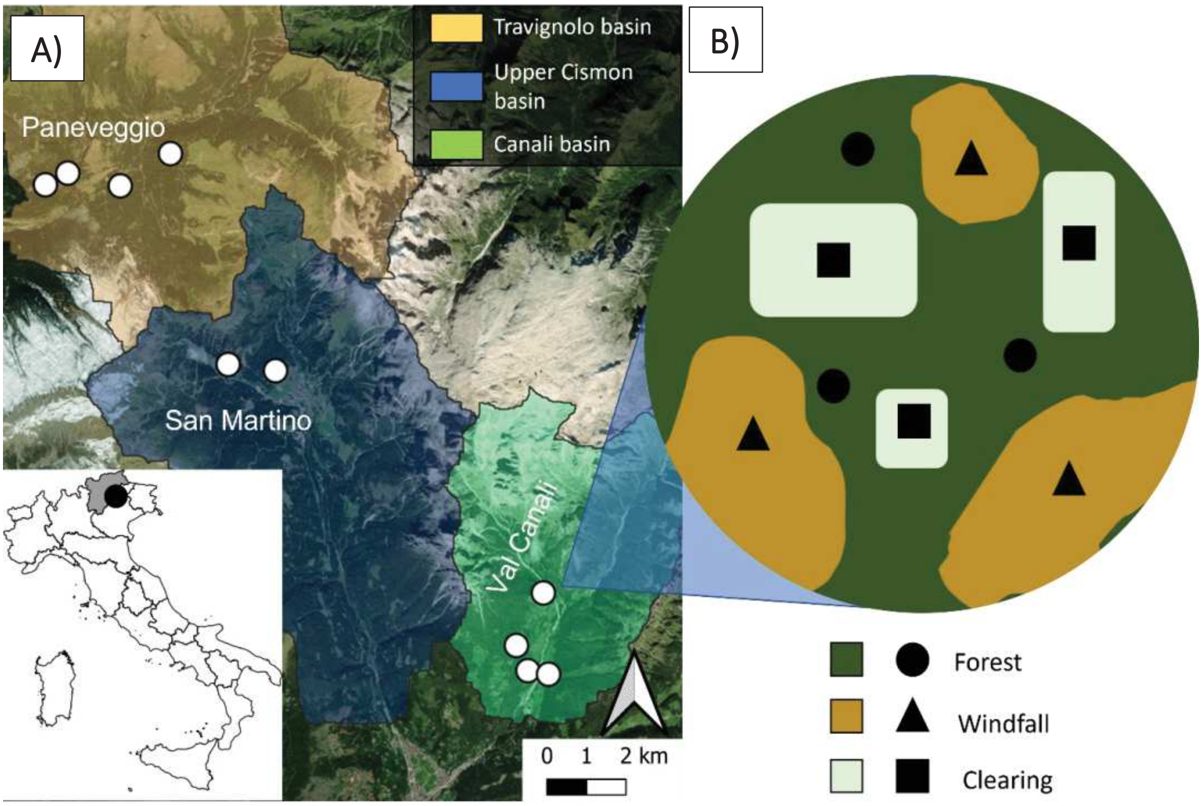

Figure 1 -Our sampling areas comprised three drainage basins (Fig. 1 A). Our ten sites are shown as white dots. Example of a study area is shown in Fig. 1 B. For each study area we selected nine sampling points: three in forest (black dots), three in windfall (black triangles), and three in old clearings (black squares).

Soil sampling and environment-DNA amplification

For each sampling point, we selected three pseudo-replicates within few meters from the sampling point. Using a clean shovel and clean gloves, we dug small pits in each pseudo-replicate, and we collected soil samples after litter removal, at 10 cm below the original surface. Soil samples from each pseudo-replicate were pooled, resulting in 2 mL of soil sample for each sampling point (15 mL of soil were also collected for backup storage). After each sampling point gloves have been changed and the shovel has been accurately cleaned from soil residuals using solvent and ethanol. Samples were kept in thermic bag with ice until lab storing at -80°C.

DNA extraction of soil samples was performed using DNeasy® PowerMax® Soil extraction kit (Qiagen, Hilden, Germany), and negative controls during extraction were used to check for contaminants. We amplified a fragment of the mitochondrial locus rps10. PCR amplification was done using a PCR nested protocol. First PCR amplification was carried out using PRV9-F (GTTGGTTAGAGTAAAAGACT) and PRV9-R (GTATACTCTAACCAACTGAGT) primers (Martin and Coffey 2012) and with following mix: 6.5

µL of water, 12.5 µL KAPA HiFi Hot Start Ready Mix, 1 µL of each primer (10 ρmol/µL), and 4 µL of extracted DNA. PCRs were run under the following conditions: one preincubation step of 95 °C for 3 min, followed by 30 cycles of 98 °C for 30 s, 58 °C for 45 s and 72 °C for 90 s, with a final extension at 72 °C for 5 min. Second PCR amplification was carried out using rps10-F (adapter-GTTGGTTAGAGYARAAGACT) and rps10-R (adapter-ATRYYTAGAAAGAYTYGAACT) primers (Foster *et al.* 2022) and with following mix: 7 µL of water, 12.5 µL KAPA HiFi Hot Start Ready Mix, 1 µL BSA, 1 µL of each primer (10 ρmol/µL), and 2.5 µL of PCR 1 product. PCRs were run under the following conditions: one preincubation step of 95 °C for 3 min, followed by 35 cycles of 98 °C for 20 s, 60 °C for 30 s and 72 °C for 60 s, with a final extension at 72 °C for 7 min. For each sample three PCR replicates were performed, and amplicon replicates were pooled together before purification step. Purification was carried out using QIAquick PCR purification kit (Qiagen, Hilden, Germany). PCR negative controls belonging to the same PCR plate were pooled. Short-read Illumina amplicon sequencing (300 bp) was performed using an Illumina NOVASEQ6000.

Demultiplexed reads were treated in bioinformatic pipeline. Primers were cut off by using CUTADAPT (Martin 2011) and reads without primers were discarded. We used denoising approach to retrieve amplicon sequence variants (ASVs). Reads were filtered, denoised, merged, and chimera were removed using DADA2 package (Callahan *et al.* 2016). For taxonomic assignment, we firstly used blastn algorithm against NCBI database to select oomycete sequences. Then, manual curation was performed to refine the taxonomic assignment. Sequences were aligned with a reference database for rps10 target gene, which was downloaded from OomyceteDB (Foster *et al.* 2022) and consists of 351 sequences of oomycetes, predominantly *Phytophthora* (144 species) and *Pythium* (133 species). ASVs with a minimum reference identity of 99% were assigned to species level.

Diversity analyses

For studying differences in species richness of oomycete communities, we used generalized linear mixed models (GLMMs) with a Poisson distribution. ASV richness was used as response variable; slope, elevation, and habitat type as explanatory variables; site ID nested in valley ID as random factor for correcting for no-independence. Also, we tested interactions between habitat type and slope, and habitat type and elevation.

Residuals were checked using DHARMA package (Harting 2021), and analysis of deviance tables were extracted with *Anova* function in CAR package (Fox and Weisberg 2019).

As multivariate exploratory analysis we used NMDS with samples aggregated by habitat and site ID. OTU table was transformed in binary matrix (presence/absence) and we used Jaccard dissimilarity index. We carried out a Redundancy Analysis (RDA) to test species composition variation against three explanatory variables: habitat type, elevation, and drainage basin ID. Pairwise comparisons among drainage basins were tested using the function *multiconstrained* in BIODIVERSITYR package (Kindt and Coe 2005).

To further investigate geographic distance, we ran MRM (Multiple Regression Matrices) analyses on data aggregated by site and habitat type using the entire dataset. Also, to exclusively test distance at finer spatial scale we used MRM with all the samples (3 habitat types x 3 replicates x 10 sites) by testing each basin separately. MRM analyses were computed by using *MRM* function in ECODIST package (Goslee and Urban 2007). All analyses were performed in R software (R Core Team 2022).

Results

Overall, we found a mean value of 45067 raw reads per sample (SD = 15488). Besides we found some reads in our negative controls, these sequences did not match with any of the sample sequences, so we proceeded with the analyses. After bioinformatic pipeline we found an average of 20763 no-chimera reads per sample (SD = 15424). After taxonomic assignment we retrieved in total 153 valid ASVs of oomycetes. The majority of sequences have been recognized at low taxonomic resolution (i.e. 68 sequences at class level; 4 at order level; 18 sequences at family level), while 48 sequences have been recognized at genus level, and 15 at species level (Fig 2). The most common genus was *Pythium* spp. (45 ASVs). We found oomycete sequences in all the collected samples.

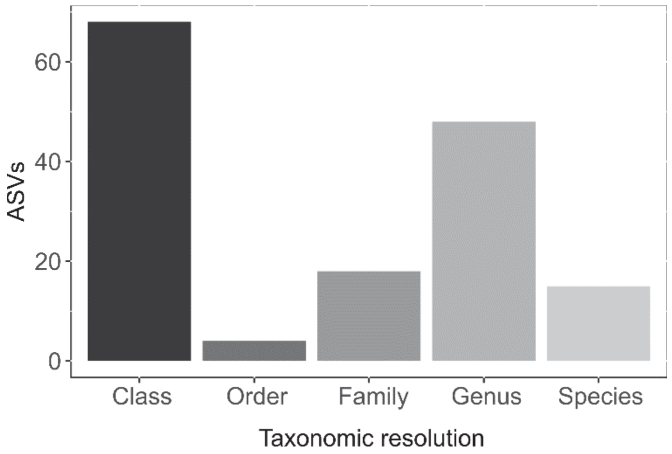

Figure 2 - Taxonomic rank distribution of the 153 oomycete ASVs.

GLMMs showed that ASV richness depended on the topography and habitat type (Fig. 3 – 4). We found that habitat type played a role in increasing oomycete ASV richness, especially on disturbed areas, i.e. windfalls (P value = 0.013). We found more oomycete ASVs in windfall rather than forest (P value = 0.009), however, pairwise comparisons showed that differences in ASV richness between forest and clearing, and clearing and windfall were not significant (P value = 0.220 and P value = 0.422, respectively) (Fig. 3). Moreover, we found higher ASV richness in communities sampled on steep slopes (P value = 0.007), whereas elevation was not significant (P value = 0.801) (Fig. 4). We did not find significant effects of interactions, so interacting terms were excluded in the final models.

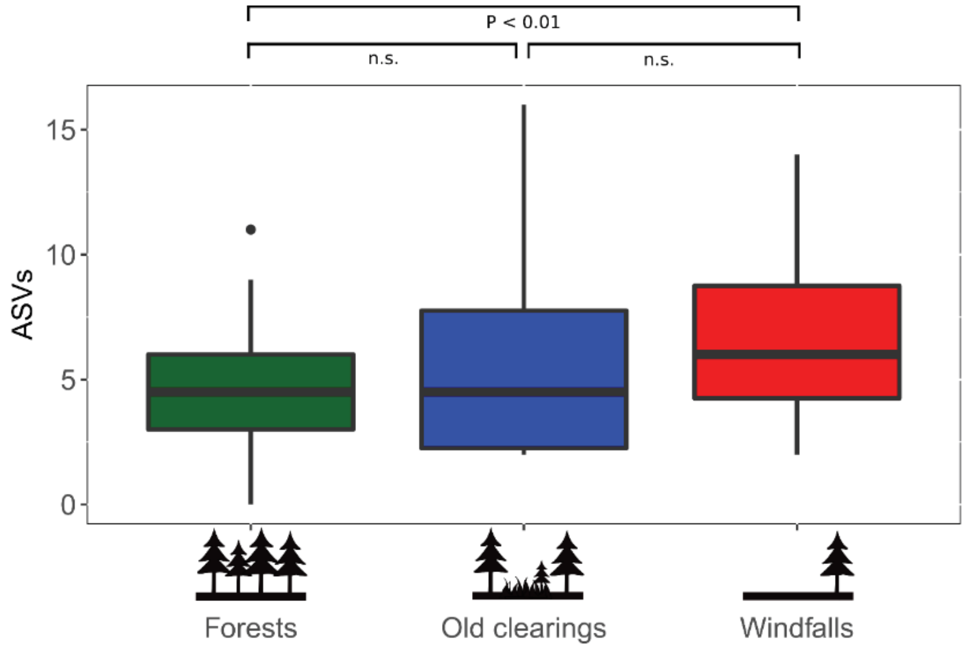

Figure 3 - Comparison of ASV richness among the three investigated habitats: forest (green boxplot), old clearings (blue boxplot), and windfall (red boxplot).

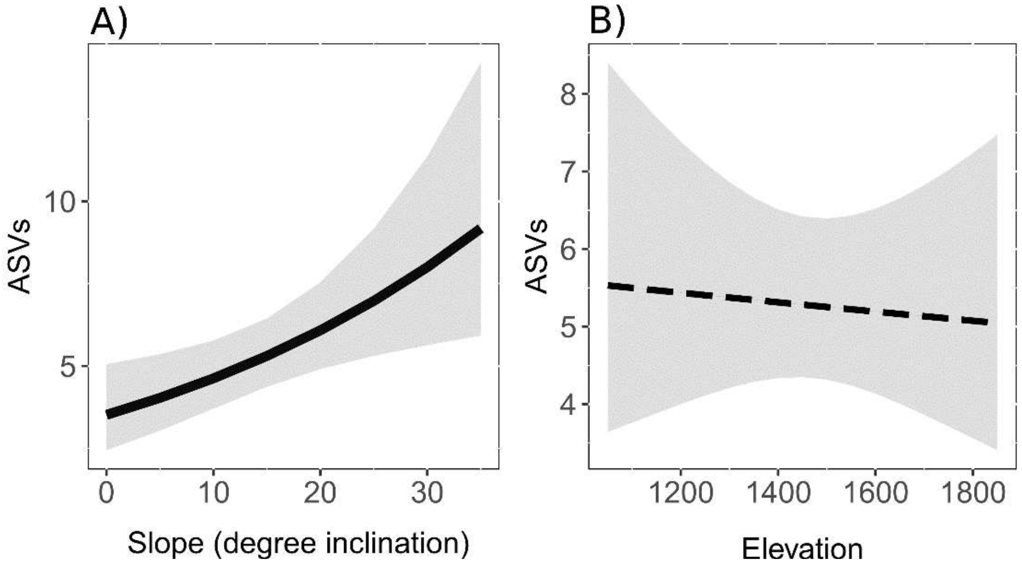

Figure 4 – Effects of topographic parameters, slope inclination (A) and elevation (B) on richness of oomycete ASVs.

Regarding species composition, we wanted to test whether oomycete communities exhibited differences in composition among habitat type and along drainage basin and elevation gradient (Fig. 5). We found that species composition did not depend on habitat type or elevation (RDA analysis, P value $_{\text{elevation}}$ = 0.161 and P value $_{\text{habitat}}$ = 0.386). However, we found that communities were clustered depending on geographic basin (P value = 0.001) at broad spatial scale (i.e. valley scale).

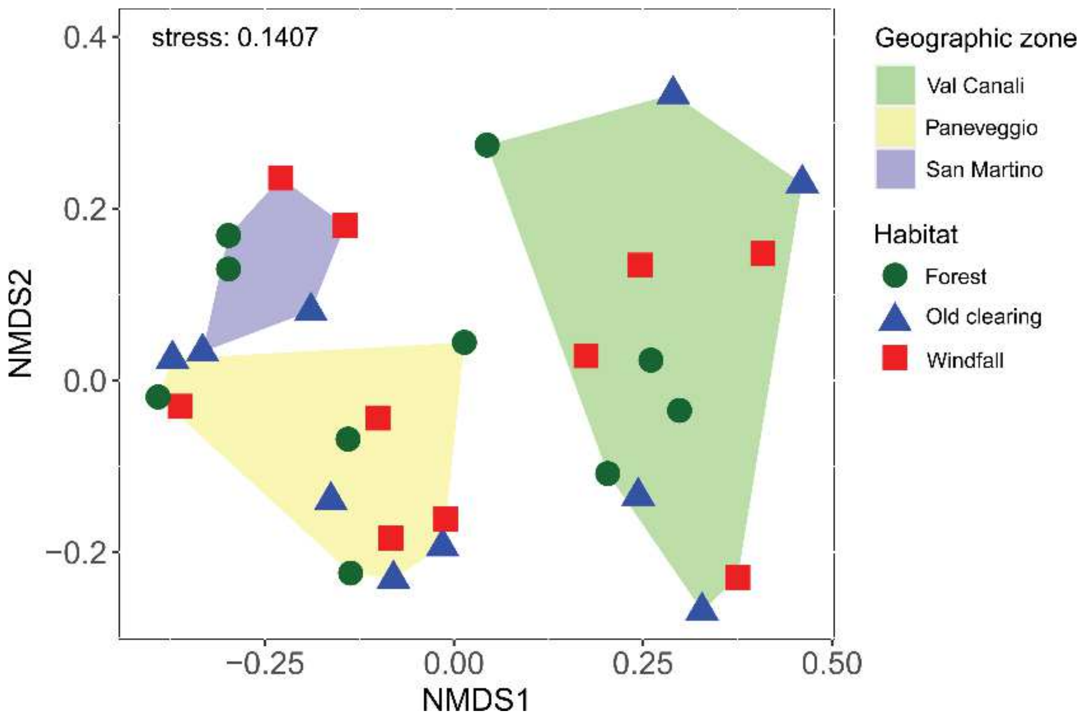

Figure 5 - NDMS plot showing dissimilarity among communities. Each point represents the aggregated community of the three sampling points within the same site and habitat. Green dots are forest samples, blue triangles are clearing samples, and red quadrats are windfall samples. Moreover, the three geographic zones (i.e. drainage basins) are shown as polygons: Val Canali in light green, Paneveggio in yellow, and San Martino in light blue.

According to MRM results, quadratic regression of geographic distance explains about 0.458 of variance (P value = 0.001) (Fig. 6). On the contrary, MRM at finer spatial scale, i.e., within each drainage basin, showed no-significant trends (within Val Canali site: P value = 0.830; within San Martino site: P value = 0.401; within Paneveggio site: P value = 0.100).

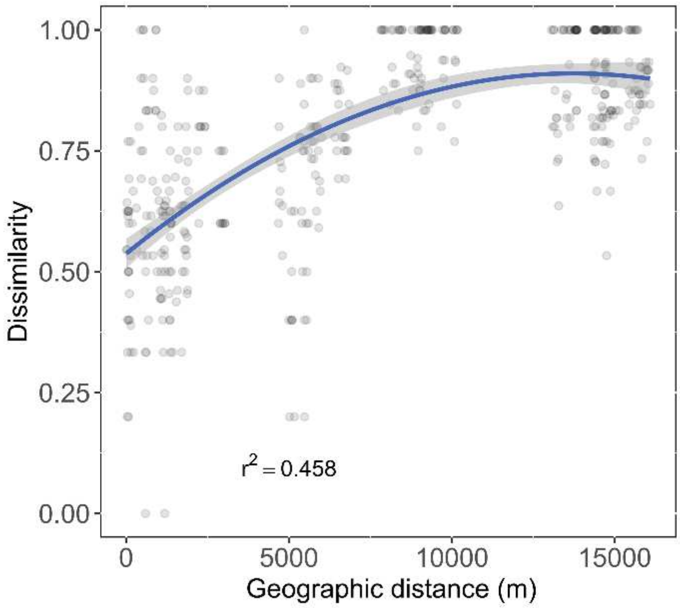

Figure 6 - MRM analysis plot. Dissimilarity was computed as Jaccard index.

Discussion

The present study represents a valuable step forward in the understanding of oomycetes diffusion in soil after disturbance in semi-natural forests. To the best of our knowledge this work is the first scientific contribution in the analysis of these organisms in the Alpine area with the use of DNA-metabarcoding. Furthermore, it is the first field research, among oomycetes metabarcoding studies, using the mitocondrial gene rps10 as molecular target for an HTS investigation. Our results clearly described two solid and original outcomes about the influence of some environmental predictors on the taxonomical richness and the communities composition of the Oomycetes: a) the habitat type and slope might affect the oomycete richness in the natural environments and b) species composition of oomycete communities respond to the drainage basin spatial scale, but not to the local scale, even among different habitats.

Habitat type and topography influence species richness

Our results showed that post-disturbance sites can host richer communities of oomycete species compared to forest, thus potentially playing a role during regeneration process. After the soil disturbance due to the wind and the salvage logging, post-disturbance soils are exposed to higher solar radiation and, consequentially, are warmer (Hashimoto and Suzuki 2004). The increasing in temperature can lead to higher microbial activity, especially regarding the organic matter decomposition, thus affecting the composition of chemical compounds in the soil (Kalbitz *et al.* 2004). Our findings agreed with other metabarcoding studies aimed at understanding the short-term responses of soil microbial and fungal communities across gradients of logging intensity in forest stands (Parladé *et al.* 2019, Danielson *et al.* 2020): saprophytes organisms increased after clear-cutting in coniferous forests. Since saprophytic fungi play an important role in the decomposition process, their activity increase with the presence of decomposing roots or retired branches after logging activity (Kyaschenko *et al.* 2017, Kohout *et al.* 2018, Mushinski *et al.* 2018). On the contrary, old clearings did not show differences with either forest or windfall habitat. Our work provided evidence that oomycete taxonomical richness, including species with a high degree of pathogenicity, might be also affected by changing environmental conditions due to both natural (e.g. windfall) and anthropogenic (e.g. salvage logging management) causes.

Moreover, we found that slope influenced the richness of omycetes. Previous studies showed that slope affects the isolation rates of *P. cinnamomi* in cork oak stands in Portugal (Moreira and Martins 2005), as well as oak rizhosphere-associated oomycete community patterns in the Spanish dehesas (Sapp *et al.* 2019). Variations in topography might be related to different edaphic conditions, such as soil depth or moisture (Sapp *et al.* 2019) or might affect species dispersing by water flow, thus influencing the infestation proceeding (Cardillo *et al.* 2018). Unfortunately, further research is needed to have a comprehensive overview of the factors affecting the species assemblaging of oomycetes. However, this finding adds an important piece to the understanding of the ecology of these microorganisms in temperate mountain environments, as part of a still barely sketched out line of research (Jung *et al.* 2019, Khaliq *et al.* 2019, 2021), and the consistency of this pattern across mountain areas should be further investigated.

The role of distance and habitat type in shaping oomycete communities

Our findings on the community composition suggested that geographic distance might play an important role in shaping oomycete communities at different spatial scales. At the fine spatial scale, oomycete species assemblages were not affected by the changing of elevation in the studied areas. This result is consistent with data from previous studies (Burgess *et al.* 2019, Khaliq *et al.* 2021) investigating the community composition of *Phytophthora* species across the Australian continent, over high variation of environmental conditions. Moreover, no differences in the species composition of oomycete communities were found in the different types of habitats, suggesting that the changes occurred in soil after the disturbances were not able to significantly influence the species composition, in spite of a slight pattern of species richness variation. Nevertheless, we found that a high variability in species composition existed, even among closed communities, suggesting a patchy distribution of species within the landscape regardless of the differences in habitat types. Previous studies investigating the presence of *Phytophthora* species using HTS techniques also showed a random occurrence and defined such organisms as "transient" in natural environments (Khaliq *et al.* 2021). However, despite the high variability among closed samples, shared species are always present within the same geographic zone (i.e. drainage basin). On the contrary, communities located at a distance of about ten kilometres were completely different. Our findings therefore suggest that the communities of oomycetes might consist in a variable mosaic of species with significant distinctions at the broad spatial scale, regardless the variability of altitude and habitat types. Besides we investigated the short-term response just after two years of the storm, we included also old open habitats (i.e. old clearings) in our sampling showing similar results. Indeed, oomycetes have greater ecological resilience than other soil microorganisms, such as bacteria (Cambi *et al.* 2017) and fungi (Hartmann *et al.* 2014), which are more sensitive to sudden changes in habitat due to forest management practices. For instance, important pathogens within this large taxonomic group (e.g. *Phytophthora* genus) can also easily survive as biotrophs within ecosystems without causing any damage (Crone *et al.* 2013, Jung *et al.* 2020, 2021). Our study supports the hypothesis that the occurrence of oomycetes in soil is mostly driven by neutral processes occurring at different spatial scales rather than selection by environmental filtering.

Conclusions

Here, we suggest that windfall habitat has the potential to host soilborne pathogens, since more species richness of oomycetes was found in those disturbed sites. However, our study highligthed that natural communities of oomycetes are rich, but mostly unknown. Thus, our findings imply the crucial need for greater future efforts in metabarcoding analysis of communities of soil-living microorganisms in post-disturbance forest environment in different climatic zones, as well as further research in oomycete taxonomy and functionality. Moreover, topography should be considered in metabarcoding studies of oomycete communities, because steepness might influence the dispersion of those organisms, and thus their occurrence.

Our results can provide useful and pratical guidance for designing surveys aimed at detecting potentially soil-born pathogens in natural mountain environments. First, given the patchy distribution of the species at the fine spatial scale, we suggest to consider a high number of samples (which could be pooled before DNA-extraction eventually) to have a better representation of the oomycete community. Second, post-disturbance sites and steep sites showed high species richness. Investigation should be prioritize in these conditions for sampling higher species richness. Third, the drainage basin spatial scale (i.e. about 5 km distance in our study area) seems to be appropriate to large scale surveys, since within each basin communities are quite similar, but they differ among different basins.

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CHAPTER IV

Drought and stand susceptibility to attacks by the European spruce bark beetle: A remote sensing approach

Davide Nardi, Hervé Jactel, Elodie Pagot, Jean-Charles Samalens, Lorenzo Marini

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Abstract

1. Several time-series analyses have demonstrated that after extreme summer drought bark beetle damage increased. However, studies predicting stand susceptibility over large spatial extents are limited by technical constraints in obtaining detailed, spatially-explicit data on infestation spot occurrence.
2. Using a unique dataset of georeferenced bark beetle infestation data, we tested whether the spatial variation of local growing conditions of forest stands, topography, and landscape variables modified the local occurrence of *Ips typographus* infestations after a severe hot drought in Central Europe.
3. Bark beetle infestation occurrence depended on soil-related aridity intensity, elevation, slope, and soil conditions. We showed that elevation interacted with growing conditions and topography. At low elevations, spruce forests growing on flat areas and wetter soils were more sensitive to the infestations. On the contrary, forests on steep slopes and soils with low water availability were rarely attacked. At the landscape scale, bark beetle damage increased with host tree cover but decreased with compositional diversity.
4. Our findings are generally consistent with the growth-differentiation balance hypothesis that predicts that trees growing under chronic dry conditions tend to be more resistant against biotic disturbances.
5. Spruce stands at low elevations located in homogeneous landscapes dominated by spruce were those more exposed to bark beetles in the initial phase of a drought-induced outbreak.

Keywords (6): aridity; dryness; landscape diversity; *Ips typographus*; topography; water limitation

Introduction

The European spruce bark beetle *Ips typographus* L. (Coleoptera: Curculionidea) is one of the most important insect pests of European forests. In the last decades, climate change has caused an increased outbreak propensity of this species causing severe economic damages to spruce forests (Marini *et al.* 2017, Hlásny, König, *et al.* 2021). Warmer climate leads to a faster development of the insect and to an increased number of generations per year (Seitner 1923, Annila 1969, Netherer and Pennerstorfer 2001). Under a warmer and drier climate also tree defence decreases due to transpiration deficits, thus increasing the vulnerability of spruce trees to bark beetle infestations (Marini *et al.* 2012, Matthews *et al.* 2018, Hlásny, König, *et al.* 2021). Although higher temperatures and drought events usually increase bark beetle damage at the regional scale, local infestations are often patchy. Many studies have tried to understand how tree or forest conditions could impact the risk of bark beetle outbreaks at the local scale (Berryman 1982, Baier 1996, Baier *et al.* 2002, Overbeck and Schmidt 2012, Blomqvist *et al.* 2018). However, studies attempting to upscale these factors at the regional scale are still rare (Trubin *et al.* 2022). Recent evidence on resistance to bark beetle suggested that climate suitability (e.g. drought) and stand conditions are important factor at large scale and they should be included in risk assessment (Jaime *et al.* 2022). However, technical constrains in obtaining detailed, spatially explicit data on bark beetle infestations over a continuous large spatial extent still exist.

Across large geographical areas, the variability in elevation, slope and aspect may increase microclimate heterogeneity due to multiple processes such as rain shading, radiation, and wind turbulences. The combination of local amount of rainfall and soil structure (e.g. water retention capacity, soil depth etc.) is also expected to shape the growing conditions of trees potentially modifying the short-term response of spruce to drought and bark beetles (Netherer *et al.* 2019). In this context, the growth-differentiation balance hypothesis (Herms and Mattson 1992) predicts that trees growing under moderate stress, i.e. on soils with limited water and nutrient availability usually allocate more resources on defences than on growth, thus increasing their resistance against bark beetles (Ferrenberg *et al.* 2015, Huang *et al.* 2019, 2020). According to this hypothesis, steep and shallow soils may induce moderate chronic water deficiency conditions increasing the constitutive defences in slow-growing trees. On the contrary, in trees growing faster on fertile soils, extreme drought might lead to carbon depletion because of unbalanced carbohydrates demand and, thus, a systemic shortage of secondary metabolites and defence compounds may occur (Netherer *et al.* 2015, Gely *et al.* 2020). However, empirical data also support opposite patterns indicating a more complex trade-off between growth and defence depending on the environmental context and species involved (Kytö *et al.* 1996, Baier *et al.* 2002).

Besides the local factors described above, landscape processes can also affect infestation probability. Since Norway spruce is the main host tree for *I. typographus*, infestation probability should be strongly influenced by spruce availability (Netherer and Nopp-Mayr 2005, Kärvemo *et al.* 2014). Also, variability in configuration and composition of the habitat mosaics can also affect local infestation occurrence (Hlásny and Turčáni 2013, de Groot *et al.* 2019). Increased landscape heterogeneity should reduce pest damage as high tree species diversity can impair the pest capacity to locate the host (Zhang and Schlyter 2004, Kärvemo *et al.* 2016) and/or increase the pressure from natural enemies (Jactel *et al.* 2021). We therefore expect that forest landscape composition can explain some of the within region spatial variability in the attacks (Jactel *et al.* 2017, Marini *et al.* 2022).

Here, we present a large-scale study to test whether the local condition of forest stands and landscape factors can explain the local occurrence of bark beetle infestations after a severe drought and heat wave that hit central European forests in summer 2017 and 2018 (Schuldt *et al.* 2020). We used a unique dataset of georeferenced spruce bark beetle infestation data obtained from a remote sensing campaign over a large area in France (103 920 km^2). Longer time-series can reveal temporal trends of the infestation patterns (e.g. Marini et al., 2017; Stadelmann et al., 2013; Trubin et al., 2022) or highlight different key drivers of the infestation depending on the different phase (i.e. incipient, outbreak, or declining) (Lausch *et al.* 2011). Instead, here, we mainly focused on the spatial effects of local growing conditions and landscape-scale factors during the early phase of a drought-induced outbreak. In particular, our main objective was to test the interacting effect of both local-scale factors (spatial variability of temperature, precipitation, topography, and soil properties) and landscape-scale factors (e.g. compositional heterogeneity, host availability) on the spatial dynamics of bark beetle attacks during the initial phase of a large outbreak. Understanding how topography, local growing conditions and landscape composition can modify the effects of local aridity on spruce susceptibility to bark beetle infestations may help predicting future forest vulnerability to climate change impacts over larger geographic areas and prioritizing surveillance efforts.

Material and methods

Study area

The study area was located in the Bourgogne-Franche-Comté and Grand Est regions, in north-eastern France, extending for more than 100 000 km^2 (Fig. 1). Spruce forests occur as large semi-natural and planted forests on hills and mountain areas as well as fragmented stands in the lowlands. The variation in elevation of spruce forests is generally low (mean = 513 m; SD = 238 m). During 2018, an outbreak of *I. typographus,* triggered by heat waves and dry conditions that occurred in 2017 and 2018, started to spread in the entire area (Département de la Santé des Forêts 2020). No large windthrows occurred in the years before 2018 and therefore the observed attacks at the regional scale were very likely caused by the hot summer droughts in 2017 and 2018.

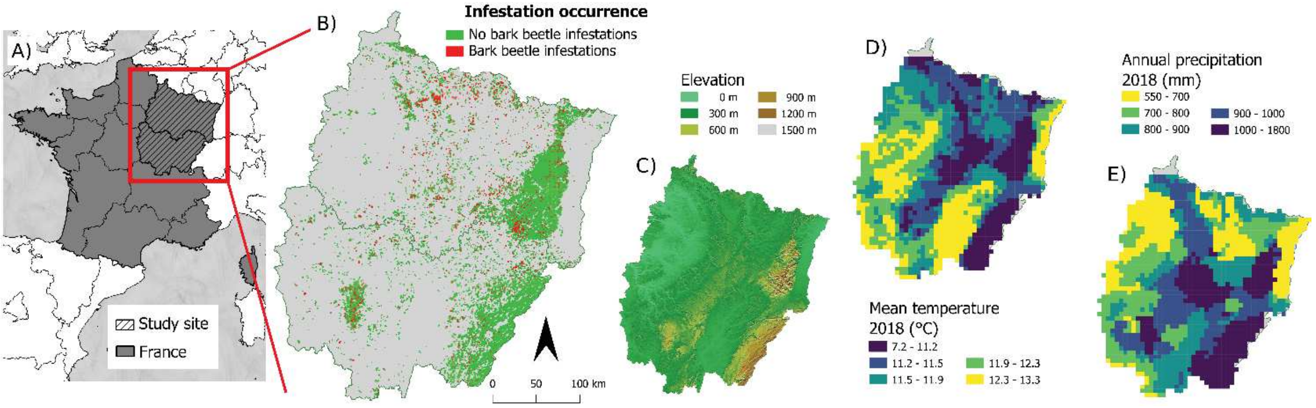

Figure 1 – Infestations of bark beetle have been continuously mapped for Bourgogne-Franche-Comté and Grand Est regions, in north-eastern France (Fig. 1 A). Spruce bark beetle infestation occurrence at 1 km cell size: cells with spruce forest and without infestations are in green, cells with infestations are in red (Fig. 1 B); Digital elevation model (Fig. 1 C), map of average annual temperature in 2018 (Fig. 1 D) and map of annual cumulated precipitation in 2018 (Fig. 1 E) are shown.

Infestation spot detection

Remote sensing detection was performed using free available Copernicus Sentinel 2 satellite images and particularly the L2A surface reflectance data products processed by CNES for the Theia data centre (www.theia-land.fr). Sentinel 2 data consist in orthorectified multispectral satellite images available as tiles (100 km x 100 km; band resolution ranged from 10 m to 20 m). Totally, 21 tiles were needed to cover the whole study area. Mapping of bark beetle spots was carried out by the processing steps listed below.

First, multispectral satellite images were collected from two time periods: February-March 2018 and February-April 2019 (see Appendix A for further details). For some tiles in 2018 more images were needed to reach a free-cloud coverage of our study area. Comparing spring 2019 with spring 2018 allowed us to depict the bark beetle infestations during the first year of the large-scale outbreak in 2018.

Second, ground observations within Grand Est province were carried out during winter 2018/2019 to detect new infestation spots. The resulting 75 sampled areas were georeferenced and polygonised using a GPS receiver.

Third, to analyse satellite data, four layers were created: a supervised classification and three inter-annual variation of spectral indices (namely the Normalized Red Index, Normalized Difference Vegetation Index, Normalized Burn Ratio) (Migas-Mazur *et al.* 2021). Ground observations were used for the initial supervised classification. After merging all four layers in a single layer, a final Support Vector Machine layer was produced and only detected *I. typographus* infestation spots having a surface greater than 0.1 ha were considered. Furthermore, to avoid false positive detections in no-spruce forests, spruce cover was retrieved from the forest type geodatabase BD Forêt (Institut National de l'Information Géographique et Forestiére 2018) and was used as a mask. Since predominant tree species were not available for many forest polygons, the following forest-type classes were selected: "spruce-fir forest" (the largely majority type), "mixture of pine and spruce-fir", "mixed forest of coniferous species without pine" and "pure exotic coniferous forest (Douglas fir) without pine" (BD Forêt codes were FF2G61-61, FF2-00-00, FF2-90-90, FF2-91-91 respectively).

Fourth, to validate the satellite detection of bark beetle infestations we used high resolution aerial survey data. Aerial survey (conducted with airplane) was carried out in 14th-15th April 2019 and 151 randomly sampled areas of 25 ha each were mapped with high-resolution images (5 cm of ground resolution). Within each sample area damaged spruce forest was present. Two hundreds seventeen polygons (8970 pixels including 899 in bark beetle damaged forests and 8071 in healthy forests) independently drawn by manual photointerpretation were used to assess the large-scale detection procedure by satellite by computing Overall Accuracy metric (Richards 2013).

Ecological variables

To deal with continuous spatial variables, we superimposed a 1 km grid. Although using a grid-based approach to aggregate spatial data is a common method, choosing the correct cell size is often a critical point. When dealing with biological spatial data, considering the scale of ecological processes can inform the selection of the data resolution (Atkinson and Tate 2000). For instance, previous studies on pest insects used the scale of insect dispersal to select the grid size (Potter *et al.* 2016). Analyses of temporal patterns suggest that infestation process mainly occurred with scale of few hundreds of meters (Kautz *et al.* 2011). However, forest fragmentation (Botterweg 1982), outbreak phase (Økland *et al.* 2016), and wind strength (Byers 2000) may increase dispersal distance up to several kilometres. Thus, a 1 km grid resolution (cell size = 1 km^2) seems to be a good compromise to study bark beetle spatial patterns and it is also comparable with some explanatory variable at coarse spatial resolution.

For each 1 km^2 cell, we estimated several explanatory variables using the zonal statistic tool in QGIS (Table 1). Digital elevation model at 25 m of spatial resolution (EU-DEM v1.1 available at https://land.copernicus.eu) was used for computing topographic variables: elevation, slope, and annual insolation. Slope and insolation were calculated in SAGA (Conrad *et al.* 2015) and output maps were cropped using spruce cover to avoid including non-spruce areas in the computation. Then, within each cell we computed the average value of each variable of interest.

Besides insolation, cumulative thermal sum is an important factor to assess bark beetle activity and the number of generations during a year. We used 8.3°C as minimum temperature and 38.9°C as maximum temperature, considering the period from 1st April 2018 to 30th September 2018 (Baier *et al.* 2007).

Soil data were used to account for different soil conditions among stands. We used map of available water content (volume fraction), hereafter AWC, at 500 m resolution (Ballabio *et al.* 2016), and soil depth at 1 km resolution (Panagos 2006).

To account for water deficiency stress, we computed April-September accumulated SPEI (Standardised Precipitation-Evapotranspiration Index) (Vicente-Serrano *et al.* 2010) in 2018. SPEI is a multiscale (it can be calculated for a specific period) and widely used index accounting for dryness (negative values) and wetness (positive values). Practically, negative values of SPEI indicate water deficiency, so SPEI decreases with aridity intensity. Since SPEI is calculated as deviation from averaging climatic conditions, we used time series of water balance (monthly precipitation – monthly potential evapotranspiration or PET) from 2011 to 2018 as input data. Temperature and precipitation data were retrieved from SAFRAN model (Durand *et al.* 2009) at 8 km resolution. Since temperature is mainly elevation-dependent, we downscaled the mean temperature at cell size by applying a standard adiabatic correction (Sheridan *et al.* 2010). PET and SPEI were computed using functions *thornthwaite* and *spei* of SPEI package (Beguería and Vicente-Serrano 2017).

To test the effect of landscape composition, we measured the proportion of spruce within each cell ("Host"). Also, we computed the proportion of mixed forest on the total amount of host cover within each cell, hereafter called Forest Diversity. Computing of landscape metrics was performed in R using LANDSCAPEMETRICS package (Hesselbarth *et al.* 2019).

Finally, we used the occurrence of a bark beetle infestation (presence/absence data) in each cell as response variable (binary). In our study, the presence of bark beetle damage in that cell occurred when at least 0.1 ha of spruce were damaged by bark beetles. Spatial and no-spatial data were managed in R 4.0 (R Core Team 2022) by using SP package (Bivand *et al.* 2013), SF package (Pebesma 2018), RASTER package (Hijmans 2020).

Table 1 - Descriptive statistics of the environmental parameters computed for 1 km each cell.

Variables	Mean	unit	Min; Max
Elevation	566	m	90; 1364
Slope	9	degree	0; 32
Available water content (AWC)	0.11	volume fraction	0.07; 0.14
SPEI	-1.46	adimensional	-1.96; -0.12
Insolation (annual)	1635	kWh / m²	1039; 2017
Thermal sum	1328	degree days	828; 1705
Soil depth	87	cm	20; 130
Host cover	29	adimensional	5; 100
Forest diversity (mixed forest proportion)	0.20	adimensional	0; 1

Statistical analyses

To avoid including cells with only marginal spruce forest along boundaries, only cells with at least 5 % (i.e. 5 ha for 1 km side cells) of spruce cover were used in statistical analyses. Because a strong correlation was found between elevation and developmental thermal sum (Pearson correlation = -0.87), only elevation was included in the models, i.e. most of the variation in developmental thermal sums was related to difference in average temperature across elevations.

A multi-model inference approach was used to evaluate alternative competing models involving climatic, topographic, and landscape variables (Burnham and Anderson 2004). In particular, we used generalized linear models (GLM) to estimate parameters with a binomial distribution (i.e. logistic models) using a maximum likelihood estimator. We ran residual autocorrelated logistic models, which are models with an additional distance-weighted function based on residuals to correct for spatial autocorrelation (Crase *et al.* 2012). We choose the greater neighbourhood distance for which Moran's I index was not significant (2 km for 1 km grid). Cells without neighbours within those distances were discarded. Then, we computed the spatial autocovariate of the residuals (RAC) by using the function *autocov_dist* in the SPDEP package (Bivand *et al.* 2013). Finally, we applied multi-model inference approach, by comparing all the possible nested models within the following global model:

Infestation occurrence (0,1) ~ Host + Forest diversity + Slope + AWC + Soil depth + SPEI + Insolation + SPEI x Insolation + SPEI x Slope + SPEI x AWC + SPEI x Soil depth + Elevation + Elevation x Slope + Elevation x Insolation + Elevation x SPEI + Elevation x AWC + Elevation x Soil depth + RAC

We tested the interactions between large scale factors, such as SPEI and elevation, and local scale factors, such as slope, AWC, soil depth, and insolation. To make estimates comparable, each included explanatory variable was standardized to mean 0 and standard deviation 0.5 using the ARM package (Gelman and Su 2020). MUMIN package (Barton 2021) was used to perform multi model selection, and MIXLM package (Liland 2021) to run models with maximum likelihood estimators. The goodness-of-fit of nested models was evaluated by second-order Akaike's criterion (AIC). The model having the minimum AIC value was considered the best-fitting model and the ranking was based on increasing difference of AIC from the best-fitting model. Usually, a cut-off value of ΔAIC = 7 is used to define a top model set and lower-ranked models were treated as less meaningful (Burnham *et al.* 2011). Furthermore, model weight (w_i) represents the relative likelihood of a model *i* and can be interpreted as the probability that model *i* is the best model. Since there was more than one plausible model, averaging estimates of predictor slopes were computed following a full model averaging approach. Here, zero was substituted into those models where a parameter was absent, and the final parameter estimate was obtained by averaging over all models in the top model set (Nakagawa and Freckleton 2011).

To evaluate potential collinearity issues among explanatory variables, we computed the variation inflation factors (VIFs) using CAR package (Fox and Weisberg 2019) on models without interactions. Since in observational ecological studies in which signals are usually weak, even a low VIF value might lead to a biased parametrisation, we used a threshold of 2. We also present correlations between the predictors included in our global models (Appendix B, Table B.1). Residual diagnostic was checked using DHARMA package (Harting 2021). Finally, ROC curve and AUC were computed to assess the goodness of fit of the binomial model in R with PROC package (Robin *et al.* 2011). AUC value varies from 0.5 (i.e. null explaining power) to 1 (i.e. model perfectly predicts data). R squared and pseudo-R squared were computed with RSQ package (Zhang 2021).

Results

General results

Bark beetle damage could effectively be mapped over the entire area as confusion matrix revealed an overall accuracy of 95% (see Appendix A, Table A.2). A total of 1659 ha (approximately 4700 spots) of damaged forests by bark beetles have been detected during 2018 (0.5% of spruce forest area). The majority of the attacks (1185 ha) was located in the northern administrative region Grand-Est, whereas 473 ha were detected in the southern administrative region, Bourgogne-Franche-Comté.

Infestation occurrence

Multi model inference on autologistic models using presence/absence data (N_{cells} = 10244, of which 1795 showed infestation occurrence) identified fifty-one models with ΔAIC < 7. Estimated effect sizes of the full averaging model are shown in Fig. 2 (see Appendix B, Table B.1 for further details). No issues in the residuals were found and the global model achieved acceptable performance (AUC = 0.82).

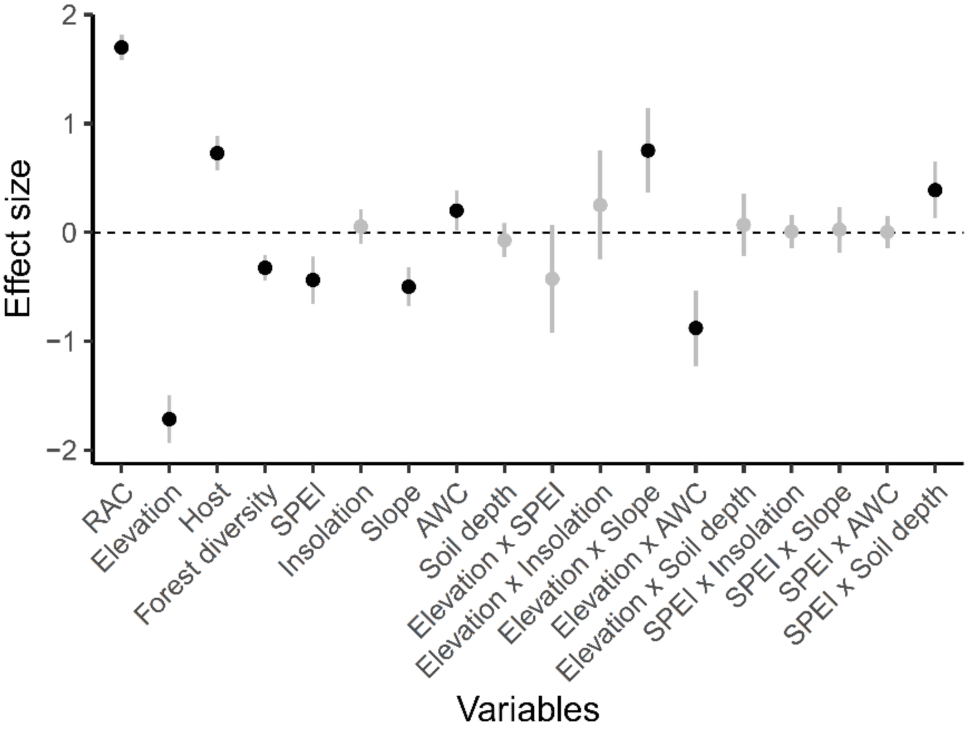

Figure 2 - Model averaged estimates and interval of confidence (95%) from the multi model selection procedure testing the effect of the predictors on the probability of infestation (binary). Black dots indicate significant effects; grey dots indicate non-significant effects (P<0.05). RAC is the residual spatial autocovariate, SPEI is the standardised precipitation-evapotranspiration index, and AWC is available water content.

Our model suggested that infestation occurrence of bark beetles was mainly driven by elevation (effect size = -1.71, P < 0.0001), showing decreasing probability of outbreak with increasing elevation (Fig. 3A-B). However, we also found significant interactions between elevation and slope and between elevation and AWC (elevation x slope interaction P < 0.001; elevation x AWC, P <0.0001), i.e. at low elevations bark beetle risk increased in flat areas, rather than on steep slopes, and also increased in soil with more water availability (Fig. 3A-B). Moreover, we found a negative relation with SPEI index (effect size = -0.44, P <0.0001), meaning that bark beetle damage probability increased with aridity. SPEI also interacted with soil depth (effect size = 0.39, P = 0.003) as we observed that bark beetle damaged increased more with aridity intensity in stands growing on shallow soils (Fig 3C). Furthermore, we found that landscape variables were important for predicting attacks. Host cover showed a positive correlation with infestation occurrence (effect size = 0.73, P = <0.0001), while forest diversity (i.e. proportion of mixed forest on the total amount of host availability) showed a negative effect (effect size = -0.33, P = <0.0001). Insolation did not act as a main driver for bark beetle occurrence. Finally, data showed a strong spatial structure, but autocovariate of residuals (RAC) successfully accounted for spatial autocorrelation (global Moran's I of the residual autocovariate model was not significant, P = 0.31).

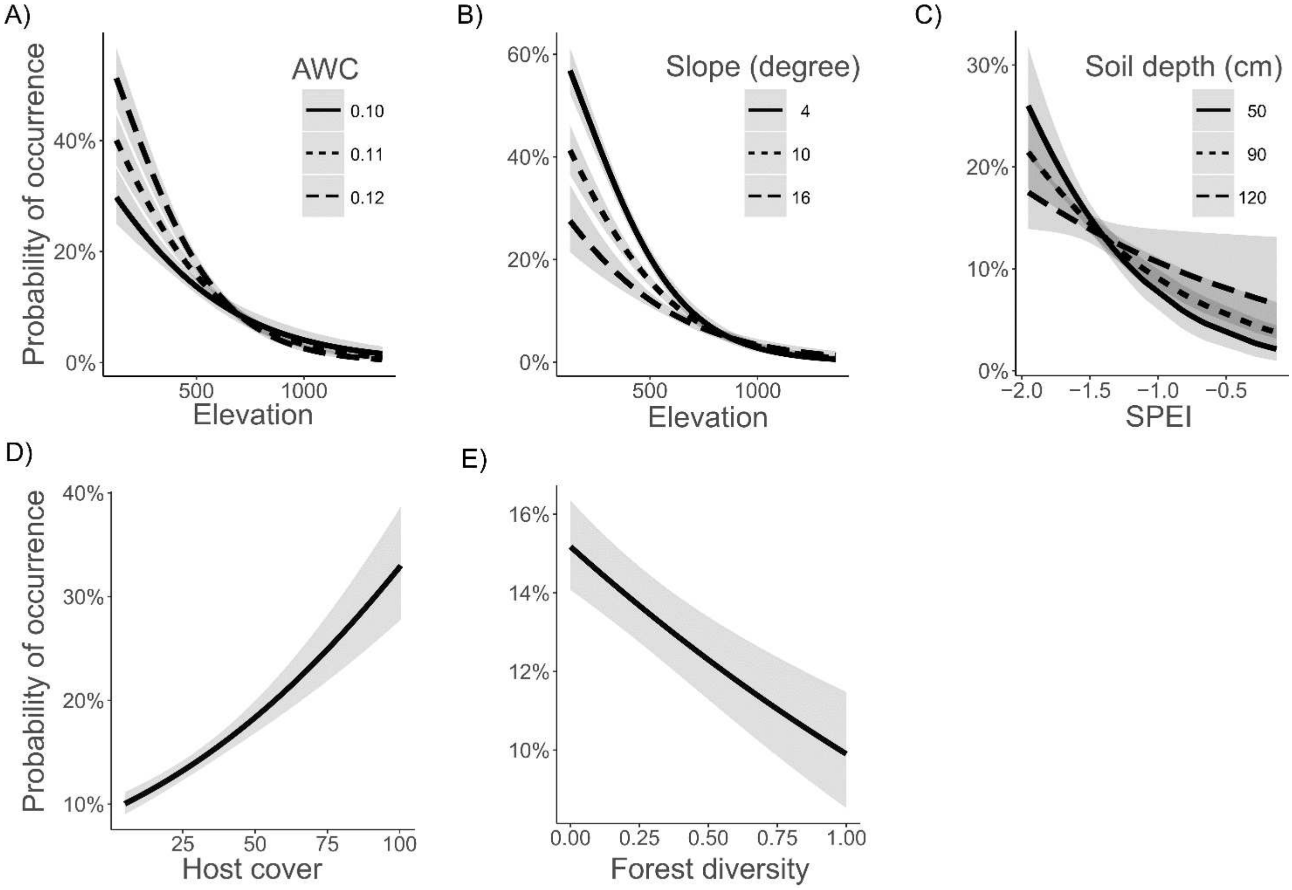

Figure 3 - Significant interacting effects on the infestation occurrence (binary) of bark beetle. Probability of bark beetle occurrence decreased with elevation, however, interactions with available water content (AWC) (Fig. 3 A) and slope (Fig. 3 B) modified the elevation effect. Negative values of SPEI (i.e. increasing aridity intensity) increased bark beetle risk, especially in stands growing on shallow soils (Fig. 3 C). Host cover increased the probability of infestations (Fig. 3 D), however proportion of mixed forest had a negative effect (Fig 3 E).

Discussion

Although a large body of research has elucidated the drivers of temporal dynamics of bark beetle outbreaks at large spatial scale (Lausch *et al.* 2011, Stadelmann *et al.* 2013, Seidl *et al.* 2016, Marini *et al.* 2017), there are still only a few studies able to explain the within-region spatial variability in bark beetle attacks (Gilbert *et al.* 2005, Kärvemo *et al.* 2014). Many previous studies have already investigated local predisposing factors to bark beetle outbreak but usually over small spatial extents (Netherer and Nopp-Mayr 2005, Lausch *et al.* 2011, Overbeck and Schmidt 2012, Pasztor *et al.* 2014, Blomqvist *et al.* 2018). However, only few dealt with stand susceptibility after severe drought at regional scale (Netherer *et al.* 2019). Using remote-sensing techniques, this study contributes to understand the occurrence of bark beetle infestations at large spatial scale by upscaling the effects of forest landscape heterogeneity, topography, local growing conditions, and aridity intensity in explaining local bark beetle damage in absence of other major triggers, such as windstorms or snowstorms. In particular, we showed that low elevation sites were more prone to be threatened by bark beetles, but also that bark beetle risk decreased in stands growing on steep slopes and on dry soils. We also found that the spatial distribution of the bark beetle was determined by landscape composition, with more damage in spruce monocultures and less in mixed forests.

Spatial variability in climate and topography

Consistently with previous studies on local predisposing factors (Lausch *et al.* 2011, Marini *et al.* 2012, Faccoli and Bernardinelli 2014), we found that risk of bark beetle attack decreased with increasing elevation. Although within our study area two generations of *I. typographus* usually occur, a third generation may occasionally develop only below 500 m (Département de la Santé des Forêts 2020). Temperature is a well-known factor of increasing bark beetle development and flight activity, thus more biotic pressure on spruce trees is expected under a warmer climate (Jönsson *et al.* 2007, Bentz *et al.* 2019, Jakoby *et al.* 2019). Consistently, we found high correlation between elevation and thermal sum, which is a well-known parameter for predicting bark beetle development (Wermelinger and Seifert 1998, 1999, Baier *et al.* 2007).

During severe drought events, elevation may also interact with local growing conditions. We found that increasing slope inclination and dryness of soil always reduced the infestation probability, especially at low elevations. Topography can change superficial soil properties by affecting transport and accumulation of solutes, and thus shaping growing vegetation (Tsui *et al.* 2004). In particular, steep slopes can be considered a good proxy for low soil water and nutrient resources because soil erosion and matter transport hamper soil fertility (Scholten *et al.* 2017). Baier *et al.* (2002) suggested that when spruce trees grow under fertile conditions, they might exhibit low defence against bark beetles and others suggested that trees growing in N-rich soils may be prone to higher pest pressure due to thicker bark (Dutilleul *et al.* 2000, Blomqvist *et al.* 2018). On the other hand, dry soil conditions can induce a moderate chronic drought status making trees more resistant and thus less prone to bark beetles attacks (Netherer *et al.* 2019). This result is consistent with the growth-differentiation balance hypothesis that predicts a trade-off between costs of secondary metabolites relative to the demand for photosynthesis by growth (Herms and Mattson 1992). Fast growing trees are expected to be less resistant to bark beetle attacks because when more resources are allocated to growth, less are available for investment in physical and chemical defences (de la Mata *et al.* 2017). In previous experimental studies, the growth-differentiation balance hypothesis on host-bark beetle systems has been supported (Baier *et al.* 2002), but also questioned (Kytö *et al.* 1996). Besides the fundamental importance of these previous studies, here we want to stress the need for large scale studies, which are able to test ecological hypotheses over wide environmental ranges. On the contrary, we found that soil depth had an opposite effect, showing increasing bark beetle infestation probability in shallow soils. A previous study (Blomqvist *et al.* 2018) has already shown higher bark beetle infestation severity in trees growing on shallow soils in spite of fertile conditions, suggesting that different soil parameters may have different importance in explaining tree susceptibility. Our results, in agreement with previous observations, seem to suggest that growth-differentiation balance hypothesis works well with certain parameters (i.e. slope and overall water capacity), but under stronger limiting factors potentially affecting resources availability (i.e. shallow soils and thin root depth) bark beetle host tree susceptibility might increase (Wild 1953).

The key role of summer drought as an outbreak trigger is well-known (Worrell 1983, Wermelinger 2004). Consistently, the spatial variability in precipitation and evapotranspiration helped us predicting the local infestation occurrence of spruce bark beetle. We found a negative effect of SPEI on infestation occurrence of the European spruce bark beetle, i.e. stands located in sites experiencing higher than average water deficiency during the summer 2018 had a higher mortality rate due to bark beetle infestations. Reduced water availability usually makes Norway spruce trees more susceptible to biotic disturbances (Netherer *et al.* 2021). However, besides the temporal effect of drought on bark beetles-host system, it is important to stress that here we aim to investigate the spatial variability of precipitation related to topography. Indeed, we observed that aridity intensity affected infestation occurrence of *I. typographus*, but this effect was modified by soil depth. Trees growing on shallow soils showed increasing bark beetle outbreak occurrence with increasing water deficiency, but no effect was observed on trees growing on deeper soils.

Finally, although solar radiation was found to be locally relevant in other studies (Kautz *et al.* 2013, Blomqvist *et al.* 2018, Mezei *et al.* 2019), we found no effect of this factor. This is probably due to the relatively flat terrain of our study area without high mountain ranges. Previous studies also found that solar radiation and aspect did not play an important role as predisposing factors of bark beetle infestations (Lausch *et al.* 2011, Kaiser *et al.* 2013), or even opposite pattern in which north-facing slopes showed higher damage (Jurc *et al.* 2006). These differences among studies might suggest that solar radiation might be more relevant under certain conditions, such as in mountain areas where strong gradients exist.

The role of the host availability and landscape heterogeneity

Besides local factors, landscape context has been revealed to be an important predictor for tree mortality during bark beetle outbreaks (Simard *et al.* 2012). We found that host availability within the cell was a strong predictor for bark beetle infestation occurrence. Our results are consistent with previous observational studies showing that higher percentage and/or volume of spruce forest at the landscape scale increased the risk of attacks (Netherer and Nopp-Mayr 2005, Kärvemo *et al.* 2014, 2016). At the landscape scale, the spatial structure of bark beetle populations is linked to host connectivity, thus increasing the risk of bark beetle damage in spruce-dominated landscape (Seidl *et al.* 2016). In addition, forest compositional diversity at the landscape scale could play a potential role in mitigating bark beetle damage due to reduced host availability and accessibility, enhanced natural enemy activity or barriers to dispersal (Hlásny and Turčáni 2013, Jactel *et al.* 2021). In accordance with these predictions, we found that the proportion of mixed forest decreased the probability of infestation occurrence, although this effect is weaker than that of host (spruce) availability. Our results thus agreed with previous studies showing the beneficial effect of mixed forests rather than monocultures when dealing with bark beetles (Kärvemo *et al.* 2014, de Groot *et al.* 2019, Sommerfeld *et al.* 2021).

Potential limitations

Our models explained relatively low proportions of total variation (~23%). Indeed, several limitations in our approach might exist. First, we could not quantify other potential key drivers using remote sensing techniques, such as stand age and structure such as density of spruce or biomass data. Second, we could not distinguish between regular harvesting and sanitary cutting, thus all cuttings were identified and indifferently removed using inter-annual vegetation indices. However, the amount of sanitary logging was relatively low during 2018 since most of the clear cuts were carried out during 2019 and 2020 (Département de la Santé des Forêts 2020, 2021). Third, our study was based on the spatial patterns of infestations during the first year after the drought event, while we cannot exclude that some of the observed effects may change with the progression of the outbreak or with drought persistence. Fourth, despite our selecting cell size (1 km^2) seemed to be the best compromise to include both broad and fine resolution variables, we missed some small-scale processes such as edge effects.

Conclusions

Because of climate change, bark beetle outbreaks are expected to increase in the coming years with severe consequences for European forest landscapes (Hlásny, König, *et al.* 2021). Although temporal dynamics of bark beetle populations have been thoroughly studied in Europe, investigations of spatial dynamics at large spatial extent are still scarce. Thanks to the availability of medium resolution satellite images, we are now able to better monitor forest disturbances across a wide geographical area and to upscale at the regional scale key risk factors to predict the first occurrence of *I. typographus* at medium spatial resolution (1 km). However, we still lack studies quantifying easily measurable physiological thresholds to predict tree susceptibility to bark beetle attacks (Baier *et al.* 2002, Blomqvist *et al.* 2018, Netherer *et al.* 2019). We thus suggest that remote sensing can be used in bark beetle monitoring as a large-scale detection tool, integrating pheromone trap data which are still valuable as local warning system (Weslien *et al.* 1989, Faccoli 2009). Finally, our study can provide useful practical outcomes for managing large outbreaks in spruce forests. In particular, it suggests that surveillance efforts after extreme drought events should be focused on stands growing at low elevations, on flat areas and on wetter soils, whereas sites exhibiting chronic stress (i.e. drier soil and steep slopes) are less prone to bark beetle damage at least during the initial phase of the outbreak. In a long-term perspective, our study suggests to avoid planting spruce stands at lower elevation plains trees might experience more pest pressure due to a warmer climate. It also highlights the need to avoid large spruce monocultures. Considering the increasing risks of summer hot droughts in the next future due to climate change, forest managers should consider both the local stand and landscape susceptibility when implementing forestry planning.

Acknowledgements

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CHAPTER V

Role of abandoned grasslands in the conservation of spider communities across heterogeneous mountain landscapes

Davide Nardi, Lorenzo Marini

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Abstract

In the last decades, the transformation of agriculture and the associated decline in semi-natural grasslands have been major drivers of the loss of spider diversity across Europe, in particular in mountain regions. In the early stages of forest succession, abandoned grasslands exhibit a complex vegetation structure sharing environmental conditions with both open habitats and forests. At the landscape scale, the occurrence of abandoned patches can potentially provide novel habitats and niches for ground-dwelling spiders. Here, we used two complementary methods: traditional species diversity analyses and species-habitat networks to understand how abandoned grasslands can interact with the surrounding habitat mosaic in supporting spider communities. We selected six landscapes along an elevational gradient and sampled spiders in all the major agricultural and semi-natural habitats occurring across the landscapes. At all elevations, we found a similar species richness and activity density between agricultural habitats (i.e. meadows, pastures, and crop fields) and abandoned grasslands. On the contrary, we consistently found lower species richness and activity density in forests than in all open habitats. Despite the similar diversity between open habitats, most species-habitat networks exhibited a high and constant modularity, i.e. the same species tended to occur in a specific habitat type and not in the others. Only a few species were shared between abandoned and agricultural habitats, indicating that abandoned grasslands cannot support populations of most species typical of open managed habitats. Early abandoned patches increased landscape habitat heterogeneity providing unique niches to spider species that, however, rarely occur in other habitats. The maintenance of multiple habitat types across the landscape is expected to increase the regional species pool, while the role of abandoned patches as surrogate habitat for the conservation of spider species typical of semi-natural grasslands appeared limited. Similarly, abandoned patches are not expected to help maintaining the populations of spider species occurring in agricultural habitats.

Keywords (5): Abandonment; Management cessation; Modularity; Predators; Species-habitat network

Introduction

In the last decades, the transformation of agriculture and the associated decline in semi-natural grasslands have been major drivers of biodiversity loss across Europe, in particular in mountain regions (Marini *et al.* 2011, Damisch *et al.* 2020, Geppert *et al.* 2020). On the one hand, agricultural specialization has led to more intensive agriculture practices in grasslands located at low elevations and on fertile soils. On the other hand, sites where mechanization is difficult due to topographic constraints (e.g. steep slopes and shallow soils) have been often abandoned (MacDonald *et al.* 2000, Stoate *et al.* 2009). The suspension of traditional management is a widespread trend in Europe and abandoned grasslands are expected to increase in the coming years (van der Zanden *et al.* 2017). Grassland abandonment is a relatively slow process whose dynamics depends on several factors such as soil fertility, climate, and composition of pre-existing vegetation (Tasser *et al.* 2007; Munroe *et al.* 2013). After management suspension, the herbaceous layer gradually becomes thicker with an increasing occurrence of shrubs and young trees, quickly reducing plant diversity (Prévosto *et al.* 2011). The suspension of management-induced disturbance can also have temporary positive effects on animal and arthropod species sensitive to disturbance due to vegetation structural changes (Marini *et al.* 2009). However, without further disturbance these transitional stages will be permanently lost leading to landscape homogenization, in particular where forest is the dominant land-use (Sitzia *et al.* 2010).

Abandonment might also have effects at larger spatial scale by shaping the spatial distribution of different habitats across the landscape. For instance, abandoned patches at different stages can contribute to increase landscape heterogeneity providing disturbance-free refugia or novel habitats related to transitional stages (Marini *et al.* 2009, Steinwandter *et al.* 2017). The presence of abandoned habitats across agricultural landscapes could therefore provide important ecosystem services such as biocontrol or pollination by supporting large populations of arthropod species that can colonize the surrounding habitats (Navarro and Pereira 2012, Rey Benayas and Bullock 2012, Boetzl *et al.* 2021, Hirschfeld and Van Acker 2021). Testing the spatial associations between abandoned grasslands, co-occurring agricultural and natural habitat patches is a complex task and require the sampling of multiple habitats across the landscape. Fortunately, tools developed from network ecological theory allow to analyse and describe such complex interactions using species-habitat networks (Marini *et al.* 2019, Nardi *et al.* 2019, Lami *et al.* 2021).

Among arthropods, spiders represent a key group because they play an important role by providing biological control as natural enemies as well as food resource for vertebrates and other predators (Wise 1993, Nyffeler and Sunderland 2003). Previous studies highlighted how spiders are dependent on local environmental parameters and microhabitats (Birkhofer *et al.* 2010, Marín *et al.* 2016, Barton *et al.* 2017). For this reason, spiders are an excellent model group to test the effect of abandonment because changes in habitat structure should influence their species assemblages. At the local scale, several studies indicate mixed effects of grassland abandonment on spider communities. While some studies found negative effects on spider diversity suggesting that small-scale cultivation and mild livestock grazing can help preserving spider habitats (Zakkak *et al.* 2014, Hilpold *et al.* 2018), others found that vegetation-dwelling spiders had the highest species richness in unmanaged patches (Hamřík and Košulič 2021). These contrasting effects call for new analyses that try to quantify the spatial relationships between abandoned patches and other co-occurring habitats across the landscape. Our general aim is to investigate the role of abandonment of formerly managed grasslands for the conservation of spider communities at the landscape scale along an elevation gradient in the Southern Alps. First, we want to test whether spider communities inhabiting abandoned grasslands differ from those inhabiting the main co-occurring habitat types (both agricultural and natural areas) across the landscapes. Second, we want to test whether these potential spatial differences in species habitat occupancy varied across different seasons. We hypothesised that transitional habitat patches (i.e. abandoned) can play a key role in enhancing landscape heterogeneity and thus spider diversity, and also provide resources for species hosted in agricultural habitats by acting as source habitat. To address these questions, we used both traditional diversity analyses and species-habitat networks (Cappellari and Marini 2021).

Materials and Methods

Study area and sampling design

The sampling was carried out in Veneto, NE Italy (11.16° E 45.73° N – 11.48° E 45.38° N, WGS 84). Since our study area showed different local climatic conditions and landscape composition along the elevation gradient, we decided to select three elevation belts with relatively homogeneous habitat composition. We selected two landscapes for each belt along an elevation gradient ranging from 200 to 1400 a.s.l. (Fig. 1). Each landscape was a square area of 1 km^2 (side length: 1 km), with less than 10% of urban areas. The first belt (low elevation) included areas at ca. 200 a.s.l. with an annual average temperature of 14.7 °C and annual rainfall of 970 mm (climatic data from the nearest meteorological station were retrieved from www.arpav.it). The low-elevation belt was characterized by extensive agricultural landscapes with both annual and perennial crops interspersed with forest and abandoned patches. The management of all selected crop fields was extensive. In this belt, forests were characterized by the prevalence of oak and chestnut. The second belt was located between 400 and 600 m a.s.l. (medium-elevation belt) and had an annual average temperature of 13.7 °C and annual rainfall of 1800 mm. The medium-elevation belt was characterized by traditionally managed meadows interspersed with forest patches. Meadows were managed with traditional low-intensive practices with one or two cuts and low fertilization (<50 kg N ha^{-1} $year^{-1}$). In this belt, forests were characterized by mixed broadleaved woods with oak, chestnut, black locust, and beech. Finally, the high-elevation belt was located between 1000 and 1400 m a.s.l. with an annual average temperature 9.5 °C and annual rainfall of 2700 mm. This belt was characterized by high-contrast landscapes where pastures represented the open managed habitats. Traditionally, pastures were grazed with cows and shrubs were regularly cleared. Nowadays, some pastures have been abandoned due to the loss of traditional dairy farming. At these elevations, forests were mostly characterized by beech woods and some secondary coniferous formations. All landscapes were heterogeneous mosaics including abandoned grasslands, forest areas (ranging from 40% to 60%) and different agricultural habitats depending on the elevation belt. Despite the different types of managed open habitats, all landscapes had abandoned areas as a consequence of grassland management suspension. Time since management suspension ranged from two to several years (maximum 5-10 years). However, selected abandoned patches were chosen according to their vegetation structure: they were all open habitats with sparse woody plants (i.e. shrubs or young trees that did not form a closed canopy).

In each landscape, we chose 12 patches representing all the existing habitat types (i.e. forests, abandoned grasslands, pastures, meadows, and crops), equally distributed across the landscapes. We always selected at least two patches for each habitat type occurring within the same landscape. The selection of landscapes and patches was firstly conducted using high resolution satellite images (Veneto region orthophotos 2015, available as WMTS service at https://idt2.regione.veneto.it/gwc/service/wmts). Site accessibility was evaluated during a field survey to validate and replace sampling points.

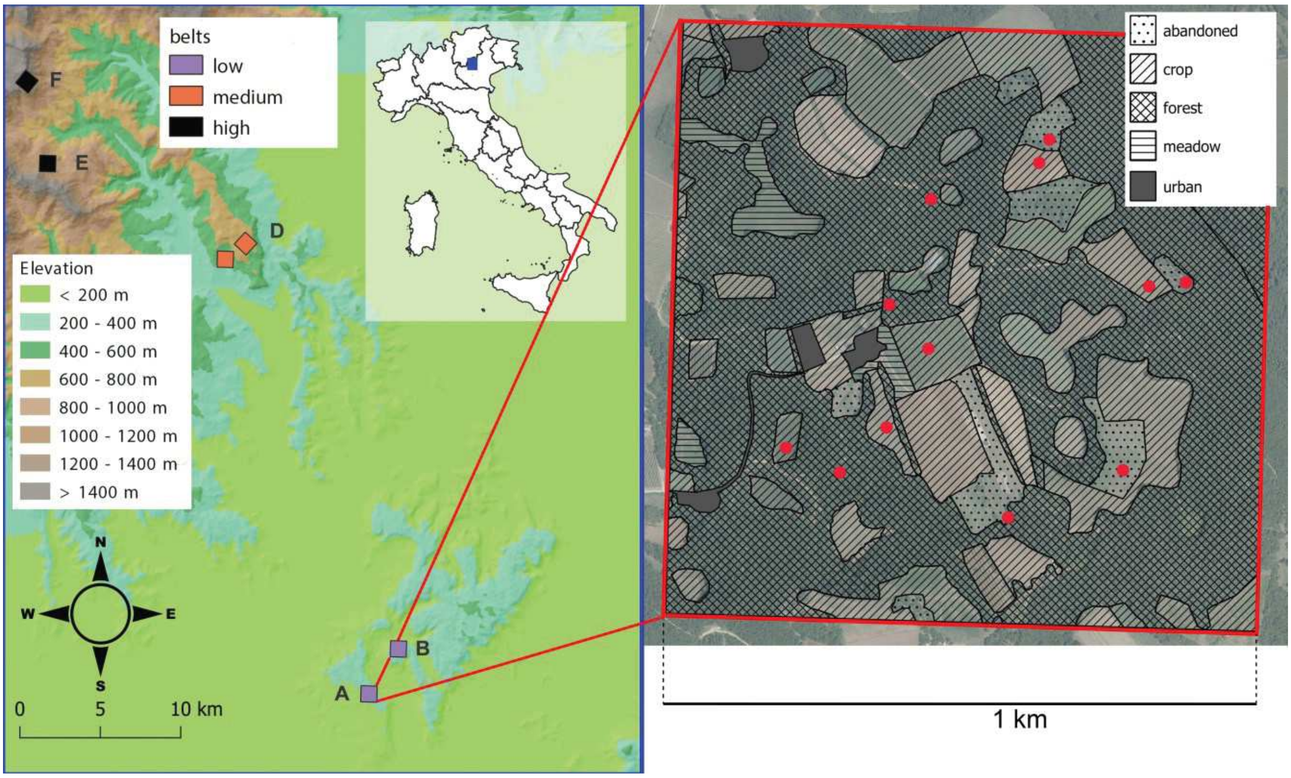

Figure 1 - Location of the six landscapes in NE Italy. We split our study area in three elevational belts accounting for different local climatic conditions and landscape composition. For each belt, two landscapes (1 km square) were chosen. For each landscape, twelve sampling points (red dots) were placed accordingly to its habitat composition. For each landscape, we sampled three categories of habitat: forest, abandoned and managed open habitat (agricultural crops in the lower elevation belt, meadows in the mid elevation belt, pastures in the higher elevation belt).

Spider sampling

For each sampling point, we placed three pitfall traps near the centre of the patch or as far as possible from the margins. Each pitfall trap was separated from the others by at least 10 m. Each pitfall traps consisted of a 0.5 L plastic cup (diameter of 10 cm, depth of 14 cm) buried in the soil and covered by a plastic plate. A wire cage (mesh size 1 cm, plastic-coated galvanized steel) was placed between soil surface and plastic plate (approximately 10 cm) to reduce small vertebrate mortality. Traps were activated for two weeks per month by using 100 ml of colourless ethylene glycol as preservative, and a drop of detergent to break superficial tension. We carried out five rounds from May to September 2019 (i.e. one round per month) during the first two weeks of each month. However, the first round was not performed at the high elevation belt because of late snowfall. Moreover, most of the traps at lower elevations were damaged by heavy rainfall events. Since the first round in May was missing at higher elevation landscapes and many traps were also damaged due to intense rainfall events at lower elevation landscapes in the first round, we decided to limit our analyses from June to

September. Collected material was stored in 75% ethanol and sorted in lab. Adult specimens were morphologically identified to the species level with a dissecting microscope. However, some individuals were identified to genus or sub-genus level. First, females of *Trochosa* sp. and *Pardosa lugubris* group cannot be easily morphologically separated (e.g. Töpfer-Hofmann et al., 2000). For that reason, we pooled females and males at a lower taxonomic resolution (genus level in the case of *Trochosa* sp. and subgenus level in the case of *Pardosa lugubris* group). Second, in the cases of *Zelotes* sp. A and *Nemesia* sp., we found individuals clearly belonging to the same species, but those are probably new taxonomic entities or a taxonomic revision of similar species is still needed. We followed the latest taxonomic nomenclature (World Spider Catalog 2021). All specimens were stored in the Natural History Museum in Bergamo or in the D.N.'s personal collection.

Statistical analyses

For each sampling point and for each round, we pooled the individuals collected by the three traps. Families with vegetation cursorial habits or weavers that are not considered ground-dwellers were excluded for statistical analyses because our sampling methods did not allow to obtain meaningful data on such groups.

Diversity analyses

To test whether habitat type and time influenced diversity metrics, we ran mixed-effects linear models. To meet model assumptions, response variables were log-transformed if necessary. For species richness and activity density, we ran separated models for each belt using habitat type and time as explanatory variables. To assess sampling effort, we computed species accumulation curves at the landscape and habitat level. All above mentioned analyses were conducted in R 3.5.2 software (R Core Team 2022) by using the following R packages: LME4 (Bates *et al.* 2015), LMERTEST (Kuznetsova *et al.* 2017), CAR (Fox and Weisberg 2019), EMMEANS (Lenth *et al.* 2020), VEGAN (Oksanen *et al.* 2020), and BIODIVERSITYR (Kindt and Coe 2005).

Community distances were calculated on overall aggregated data by using Bray-Curtis index in a non-metric Multidimensional Scaling analysis. To test whether different habitats hosted different species communities, we ran a PERMANOVA analysis using landscape ID as block effect. Then, a pairwise post-hoc test was performed by using *pairwise.adonis2* function (Arbizu 2020). To test for spatial autocorrelation in species composition, we computed an MRM analysis for each network per month by using ECODIST package (Goslee and Urban 2007).

Additionally, to highlight differences at family taxonomic level across habitat types we ran a non-metric Multidimensional Scaling analysis by averaging abundance data for each habitat type within landscape. We considered families with at least 100 sampled individuals to focus on general trends at family taxonomic level. PERMANOVA was used to assess the significance of community differentiation at family level across different habitat types.

Network analyses

We applied the species-habitat network framework to investigate both network and node level metrics (the networks for each landscape were provided in Fig. 4). Before computing network metrics, singletons (i.e. species with a single occurrence in a landscape per round) were excluded. To investigate the overall structure of our species-habitat networks, we used modularity. Modularity measures the tendency of a network to have compartments, i.e. some species and habitat patches are linked more strongly with each other than with the rest of the network (Olesen *et al.* 2007). Since our networks were quantitative, we used the DIRTLPAwb + algorithm and we computed the normalised version of modularity for accounting for biases due to network size and number of links (Beckett 2016). To evaluate modularity significance, we compared raw modularity of our observed networks with those calculated by null models as suggested by Dormann & Strauss (2014). We computed 100 randomisations for each network by applying r2d algorithm (Patefield 1981), then *z*-score were calculated. To test whether modules were mostly composed of patches belonging to the same habitat, we used the Agreement index (Lami *et al.* 2021). Then, observed values were compared with a null model, obtained by computing 100 matrices whose habitat type labels were randomly permutated, using an overlapping index, η implemented in the OVERLAPPING package (Pastore and Calcagnì 2019). Since Agreement index is normalised by the maximum values that it can take within a network, its range of values is 0-1. High agreement values, i.e. approaching 1, indicate that the modules are composed of patches belonging to the same habitat.

To investigate the role of abandoned patches in supporting species potentially occurring in other habitats, we computed the Müller index. Although Müller index has been developed to study apparent competition in host-parasitoids networks (Müller *et al.* 1999), it is a useful metric also to investigate the potential of any indirect influence (Carvalheiro *et al.* 2014). In species-habitat networks, Müller index quantifies how much one "source" patch contributes to provide resources to species occurring in other "sink" patches at landscape scale. First, we selected abandoned patches as source, then we computed pairwise influences for each patch with the co-occurring patches in the same landscape. For each network, round, and sink habitat patch, we computed the mean value of Müller index of the single abandoned patches. Log transformation was applied to achieve normal distribution. We used linear mixed effect models to assess the influence of abandoned patches (i.e. Müller index) with habitat type and time. We used habitat type and time as fixed effect, and "patch ID" nested within "landscape ID" as random effect to account for spatial dependencies. We computed a model for each belt, separately. ANOVA and Tukey post-hoc test were used to assess differences of abandoned influence among habitat types.

All above mentioned analyses were conducted in R software (R Core Team 2022) by using the following R packages: LME4 (Bates *et al.* 2015), LMERTEST (Kuznetsova *et al.* 2017), CAR (Fox and Weisberg 2019), EMMEANS (Lenth *et al.* 2020), and BIPARTITE package (Dormann *et al.* 2008).

Results

General results

We collected 9,768 specimens of ground-dwelling spiders: 8,022 adults belonging to 186 species (26 families) were determined at species level or at genus level in the cases of particularly problematic groups (e.g. females of *Trochosa* genus), while 1,763 juveniles were discarded and not considered for the analyses. Species list and sampling effort are provided as supplementary material (Appendix C). However, only 8,005 adults belonging to 172 species (22 families) were used in statistical analyses because of their ground-dwelling habits. Thus, individuals belonging to families Anyphaenidae, Cheiracanthiidae, Clubionidae, Nesticidae and to genus *Philodromus* were not considered in the following analyses. The shapes of accumulation curves suggested a consistent sampling effort across landscapes and habitat types (Appendix A).

Diversity analyses

As general trend, we found that both richness and activity density decreased over time for all belts (Table 1). Open agricultural habitat patches hosted more species in early summer than in late summer in all belts. For species richness, we observed more species in open habitat patches than in forest patches in all landscapes, but no differences were found between abandoned and agricultural managed habitat (Figs 2a, b, c). For activity density, less individuals were found in forests than in the other habitats and the difference was higher in medium and high-elevation belts (Figs 2d, e, f). In addition, during June and July at high elevation belt, pastures and abandoned patches, as opposed to the forest, showed a peak in activity density.

Table 1 - Results of the linear mixed effects models on diversity metrics. Within each elevation belt, two models were computed considering different response variables (activity density and species richness). We included habitat type and round and their interaction as fixed effects and landscape as ID a random effect. P-values from F-test were reported. If the interaction between fixed effects was not significant, we removed it and refitted the model with only the main effects.

Belt	Response variable	Fixed effects	P-value
Low	Activity density	Habitat type	0.012
		Round	<0.001
		Habitat type x Round	ns
	Richness	Habitat type	<0.001
		Round	<0.001
		Habitat type x Round	0.016
Medium	Activity density	Habitat type	<0.001
		Round	<0.001
		Habitat type x Round	ns
	Richness	Habitat type	<0.001
		Round	<0.001
		Habitat type x Round	0.058
High	Activity density	Habitat type	<0.001
		Round	<0.001
		Habitat type x Round	<0.001
	Richness	Habitat type	<0.001
		Round	<0.001
		Habitat type x Round	<0.001

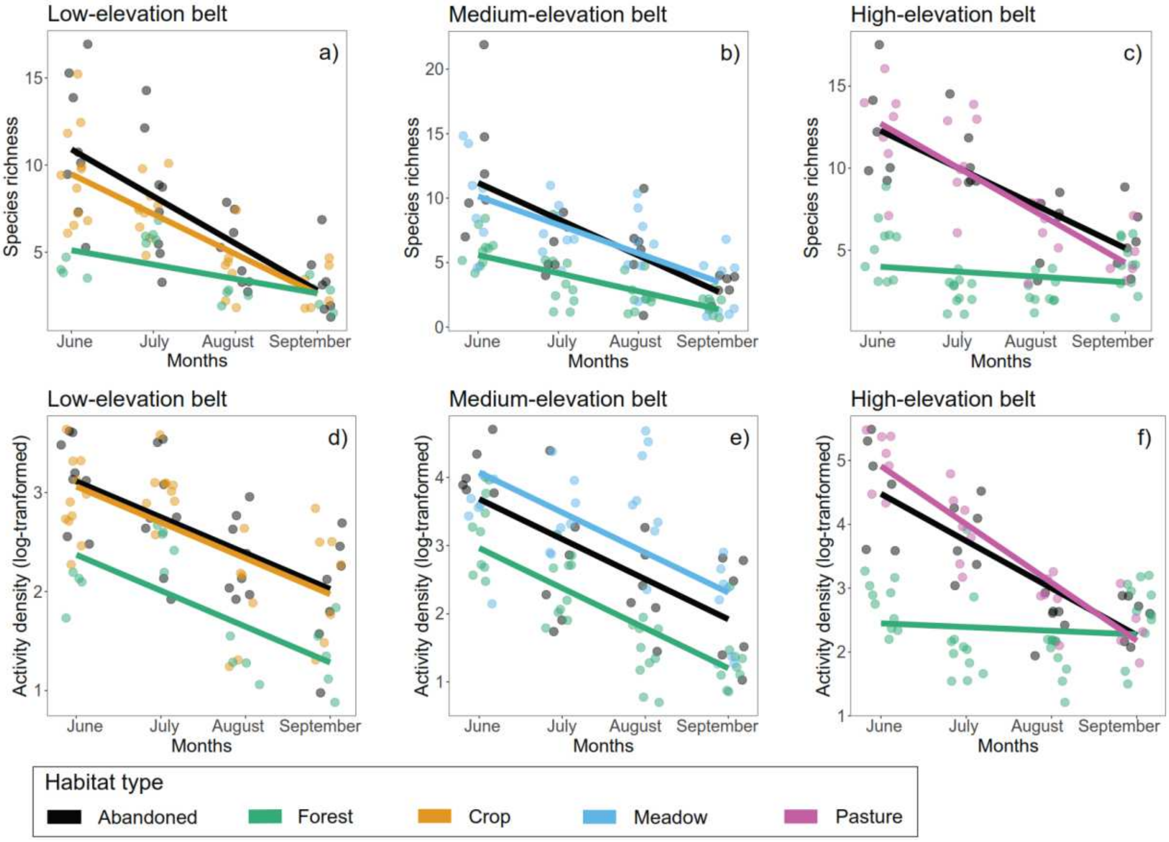

Figure 2 - Effects of time (month of sampling) and habitat type on species richness (Fig. 2 a, b, c) and activity density (Fig. 2 d, e, f). Colour of regression lines indicates different habitats. Common negative trend was found both for richness and activity density for all belts. Activity density was log transformed. Species richness (number of species) and activity density (number of individuals) were obtained by pooling the three pitfall traps.

Non-metric Multidimensional Scaling analysis at species level revealed that different habitat types hosted different spider communities (Fig. 3). Habitat type explained large proportions of variation in community composition (low-elevation belt, $R^2 = 0.23$, $p < 0.001$; medium-elevation belt, $R^2 = 0.44$, $p < 0.001$; high-elevation belt, $R^2 = 0.55$, $p < 0.001$). In all belts, communities inhabiting forests, abandoned, and managed habitats (i.e. crops, meadows, pastures) were significantly different among them (pairwise adonis, $p < 0.019$). In addition, within each belt, there was higher dissimilarity between forest and open habitats than between abandoned and managed habitats (Table 2).

Table 2 - Results of pairwise comparisons based on the adonis model. Within each elevation belt, adonis models were computed using Bray-Curtis distance. Pairwise tests were computed to assess compositional differences among habitat types. All multivariate analyses were performed considering landscape IDs as strata.

Belt	Pairwise comparison	df	F	R^2	P-value
Low	Abandoned – Forest	12	4.13	0.27	0.002
Low	Abandoned – Crop	18	1.87	0.10	0.009
Low	Forest – Crop	15	4.13	0.23	0.002
Medium	Abandoned - Forest	15	8.00	0.36	0.001
Medium	Abandoned – Meadow	13	3.88	0.24	0.001
Medium	Forest – Meadow	17	11.51	0.42	0.001
High	Abandoned – Forest	16	11.37	0.43	0.001
High	Abandoned – Pasture	12	1.87	0.15	0.018
High	Forest – Pasture	17	23.72	0.60	0.001

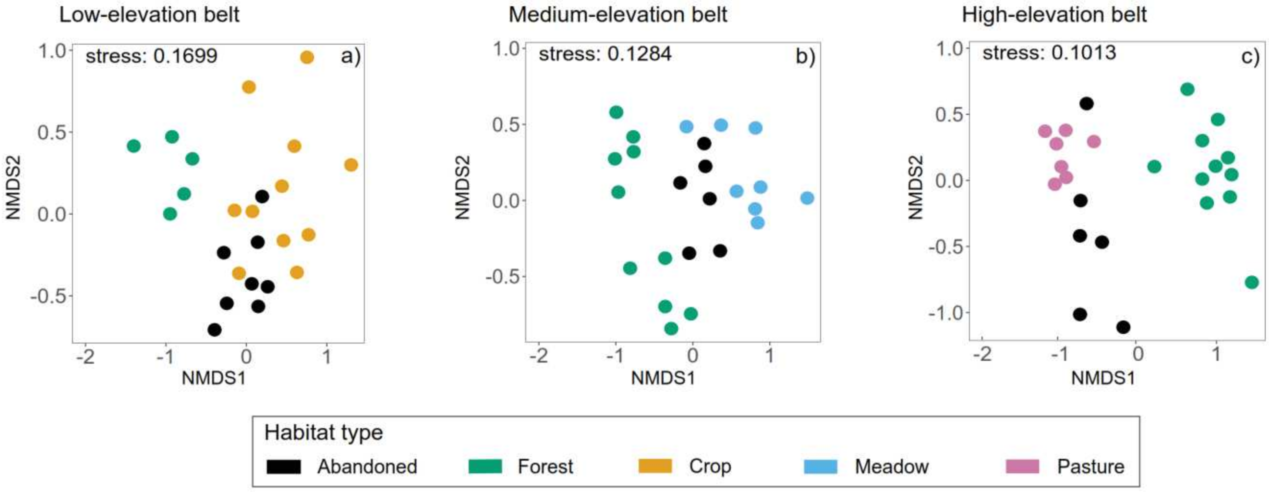

Figure 3 - Non-metric Multidimensional Scaling analyses based on Bray-Curtis distance for low- medium and high-elevation belt (Fig. 3 a, b, and c, respectively). Seasonal aggregated communities for each sampling point are plotted along NMDS1 and NMDS2 axes. Colour of points indicates different habitats.

Non-metric Multidimensional Scaling analysis at family level pointed out clear trends across habitat types even at broader taxonomic resolution (Appendix D). Habitat type explained 61% of variance and some families were strictly associated with specific habitat type: forests showed high abundance of Dysderidae and Agelenidae while Gnaphosidae were more abundant in abandoned patches at low elevation. Finally, Thomisidae mostly inhabited pastures and meadows.

Species-habitat network analyses

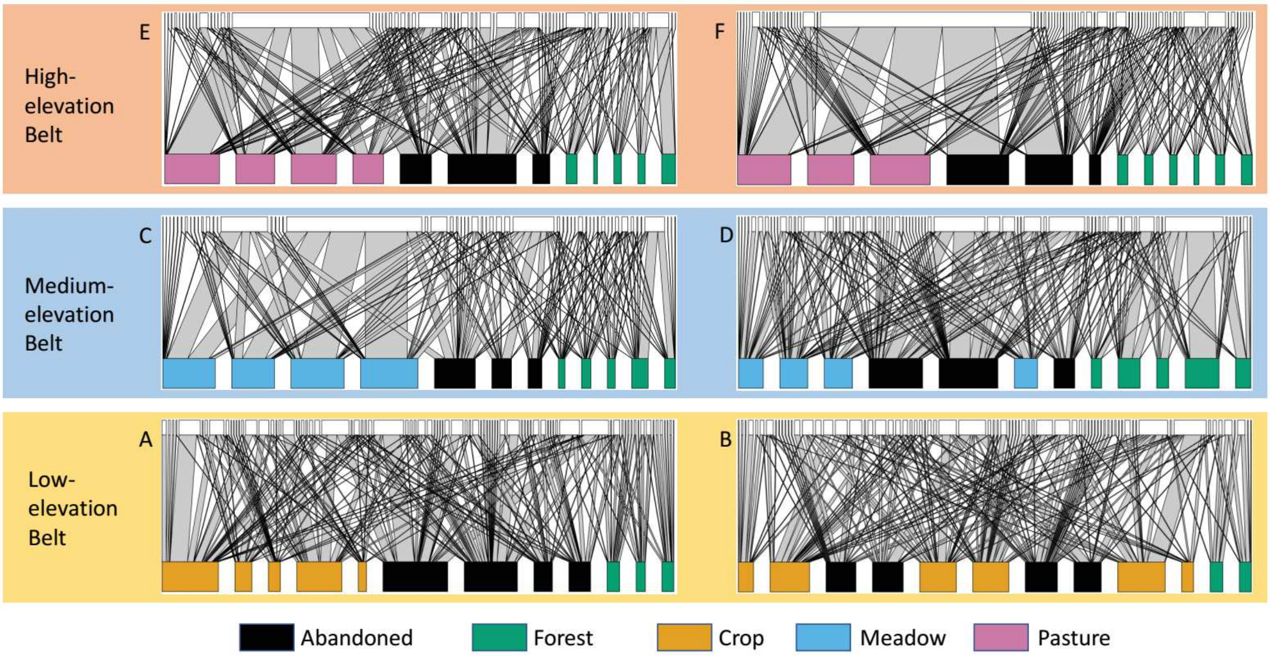

Figure 4 - Species-habitat networks for each landscape using seasonal aggregated data. In each landscape, upper rectangles represent spider species while lower rectangles represent habitat patches. Colour of rectangles at the bottom indicates different habitats. Links between upper and lower levels are weighted according to the abundance.

Except for network B in July (MRM, $p = 0.03$), we did not find spatial autocorrelation among sampling points within each network (MRM, $p > 0.05$). Normalised modularity values were high and stable over time in most of our networks (mean = 0.62, SD = 0.12). Indeed, we found that modularity was higher than expected by chance by comparing observed values with those from null models (all z-scores > 3.6), except for landscape B in September (z-score = -0.37). Average agreement index was also high (mean = 0.85, SD = 0.09), indicating that most modules were composed by patches belonging to the same habitat. Furthermore, Agreement index medians were higher than those computed using null models, except for landscape A and B in June, and B in September (Appendix B). The overlap between the observed and null distributions was low (mean = 0.25, SD = 0.26).

The influence of abandoned patches (i.e. Müller index) on the other habitats did not change over time (Table 3). On the contrary, the effect of habitat type of sink patches was significant for all belts. In particular, the influence of abandoned patches was higher for the other abandoned patches and lower for forest patches (Fig. 5b, $p < 0.01$). In the lower belt, crops were less influenced by abandoned patches than other abandoned patches (Tukey test, $p < 0.01$) but there was no difference with forests (Tukey test, $p = 0.46$). In the medium belt, meadows were more influenced by abandoned patches than forests (Tukey test, $p = 0.02$) but did not differ from the other abandoned patches. In the upper belt, pastures were more influenced by abandoned habitat than forests (Tukey test, $p = < 0.001$) but did not differ from the other abandoned patches.

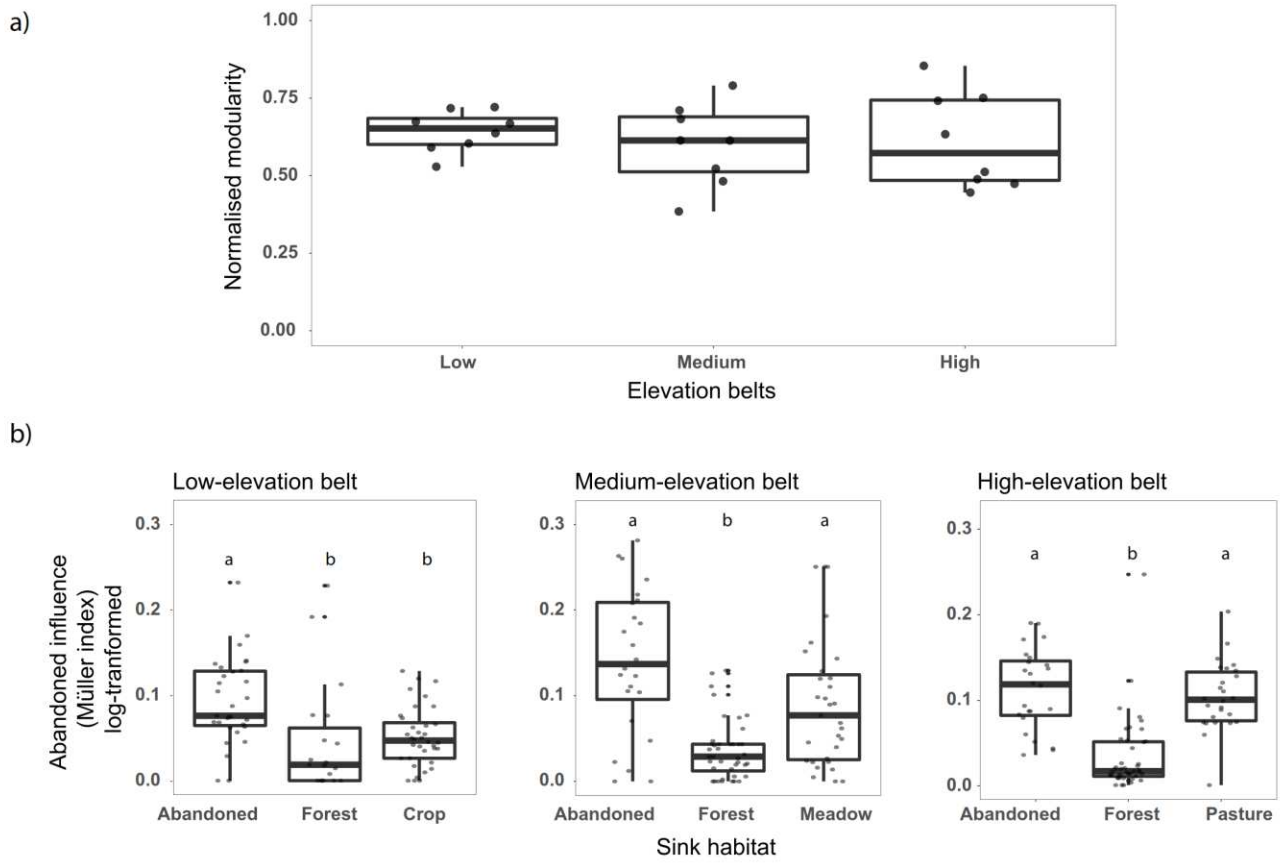

Figure 5 - Boxplot of normalised modularity for each elevation belt (Fig. 5 a), and boxplot of the Müller index quantifying the influence of abandoned patches on the other habitat types for the three elevation belts, separately (Fig. 5 b). High values of Müller index indicate that abandoned patches supported many species occurring in the sink habitat patch. Letters within boxplots indicate significant differences based on Tukey post hoc pairwise test ($\alpha=0.05$). Tests were computed for each elevation belt, separately.

Table 3 - Results of linear mixed effects models testing the effect of habitat type and round on Müller index of abandoned patches. Within each elevation belt, a LMM (Linear Mixed-effect Model) was fitted testing "habitat type", "round" and their interaction as fixed effects. Since no significant interactions were found, we ran models without interactions. P-values from ANOVA test were reported.

Belt	Fixed effects	P-value
Low	Habitat type	<0.001
	Round	0.229
Medium	Habitat type	<0.001
	Round	0.007
High	Habitat type	<0.001
	Round	0.729

Discussion

By upscaling the community sampling at the landscape scale, our study is one of the first attempts to explicitly study the role of abandoned habitats in supporting spiders across heterogeneous landscapes at large spatial scale. Here, both traditional diversity metric analyses and recently developed species-habitat networks have been used to elucidate the role of abandoned habitats in sustaining spider communities. We found that the presence of abandoned patches might play a key role in supporting spider diversity by providing unique niches compared to the other habitats occurring across the same landscapes. Different habitat types hosted distinct spider communities, and abandoned patches supported only a few species occurring in open agricultural habitats.

Diversity patterns

At all elevations, species richness and activity density in agricultural habitats (i.e. meadows, pastures, and crop fields) and in abandoned patches were similar. On the contrary, we consistently found lower species richness and activity density in forests than in all agricultural habitats. Our findings were in accordance to others studies comparing diversity patterns between different habitat types (Oxbrough *et al.* 2006, Zakkak *et al.* 2014, Nardi *et al.* 2019). However, several studies also found higher species richness in abandoned grasslands than in agricultural habitats (Theron *et al.* 2020a). As all our crop fields, meadows, and pastures were extensively managed, these traditional or extensive practices might have promoted spider species richness and abundance (Zakkak *et al.* 2014, Lyons *et al.* 2018). The species richness differences between habitats were consistent over time, while we found a general negative temporal trend in species richness and activity density towards the late summer. The first two rounds in June and July were characterized by higher species richness and higher activity density, especially in agricultural habitats. This pattern was due to the demographical peak of some wolf spiders belonging to *Pardosa* genus during early summer. High density of these ground active spiders has been already observed in other studies in grasslands (Kiss and Samu 2005) or clear-cuts during early summer (Pearce *et al.* 2004).

Modularity of species-habitat networks

Despite the similar species richness between open habitats, ordination analysis pointed out that each habitat type differs in terms of species identity and proportions from the other habitat types. In particular, there was a clear distinction between abandoned patches, forests, and open managed habitat types. Spider communities are known to be shaped by local environmental conditions (Pearce *et al.* 2004, Knapp and Řezáč 2015, Aisen *et al.* 2017), such as vegetation structure, moisture, and shading (Entling *et al.* 2007). Thus, abandoned habitats may provide novel niches that are available neither in forests nor in agricultural habitats (see also ungrazed grasslands in Lyons *et al.* 2018). Accordingly, the species-habitat network analysis confirmed high modularity. In graph theory, modularity describes whether a network is structured into subgroups of species that are internally highly interlinked (Olesen *et al.* 2007). In our habitat networks, the observed high modularity indicates that some habitat patches were tightly connected to other patches of the same habitat through shared species. In our case, high species habitat specialization seems to be the most relevant driver of the observed high modularity (Lami *et al.* 2021). Microclimatic factors, in particular, are known to be important drivers shaping β-diversity of spiders, especially across open habitats, underlining the importance of preserving wide environmental gradients in moisture and temperature conditions to maintain large regional species pool (Entling *et al.* 2007). Indeed, even small patches of different habitats might sustain distinct communities, thus promoting high diversity at the landscape scale (Theron *et al.* 2020b). However, we sometimes observed no agreement between habitat identity and modules in the low-elevation belt. One potential explanation is that the higher degree of disturbance at low elevations might have increased the presence of habitat generalists compared to the mid and high elevation belts where intensive crops were not present (Gámez-Virués *et al.* 2015). Moreover, biotic contagious processes such as dispersal between neighbouring patches might also contribute to reduce compositional differences. Accordingly, significant spatial autocorrelation was observed in some networks at low elevations indicating that neighbouring patches were more similar irrespective of their habitat similarity.

At the family level, the clear differences in community composition may reflect different functional strategies and adaptations that tend to be conserved within the same family (Cardoso *et al.* 2011). For instance, Dysderidae are diet specialists that are strictly related to forests, where their preys (i.e. woodlice) can be easily found. Linyphiidae, Thomisidae and Lycosidae were related to open habitats since these families are frequent or occasional ballooners (Blandenier 2009). We hypothesised that open habitat structure may facilitate the dispersal activity of such families contributing to their successful dispersal. Concerning the habitat effects, abandoned patches appeared to host spider communities functionally similar to those hosted by agricultural habitats while forests patches represented a clearly distinct cluster.

Potential influence of abandoned grasslands on other habitats

Despite the strong modular structure and the role of habitat type in species community assembly, different habitats across the same landscape also shared some species. To elucidate how different patches can spatially interact, we further evaluated the influence of the abandoned patches on other habitats using the Müller index. Abandoned patches supported some species occurring also in agricultural open habitats while there was very little overlap between forests and abandoned patches. Because most of our abandoned grasslands were in an early succession stage, their vegetation structure was still more similar to an open habitat than to a forest. For this reason, we hypothesised that our abandoned patches may partially act as source habitat for managed habitats. Indeed, studies investigating spider movement between different habitats confirmed that only structurally similar habitats promote spill-over between patches (Birkhofer *et al.* 2018, Michalko and Birkhofer 2021). However, our results showed that the community similarity was relatively low indicating that the dense sward found in abandoned patches probably created different microclimatic conditions and shading compared to mown or grazed grasslands or perennial crops (Entling *et al.* 2007, Muff *et al.* 2009, Košulič *et al.* 2016). These findings suggested that niche filtering was strongly relevant for spider species assemblages, reducing spider spill-over from abandoned habitats. Additionally, we did not find any strong temporal variation in habitat influence. Even if activity density and species richness changed over time, abandoned patches maintained their role as potential source habitat for open managed habitats over different seasons. As immature individuals could not be determined, one limitation of our study is that we could only focus on adults. In future studies, investigating also mobile juvenile phases might highlight differences in their habitat use (Takada and Miyashita 2014). Moreover, we focused on complex landscapes, so our findings need to be tested also in more simplified landscapes since arthropod communities may respond differently across landscape intensification gradients (Guariento *et al.* 2020).

Conclusions

Spiders are one of the most important groups of natural enemies in agroecosystems and a full understanding of the way spiders use different habitats across the same landscape mosaic is pivotal for deriving effective conservation of biodiversity and ecosystem services. On the one hand, we showed that spider communities in abandoned, agricultural habitats and forests were clearly distinct, suggesting that even weak changes in vegetation structure might cause important shifts in spider species composition. Thus, abandoned transitional patches enhanced regional diversity of spiders by providing unique habitat niches. On the other hand, the role of abandoned patches as surrogate habitat for the conservation of spider species strictly associated with semi-natural grasslands appeared limited. Similarly, the potential role of abandoned patches in supporting species found in agricultural habitats appears small, since spill-over of species between managed and non-managed habitats appears limited.

Acknowledgements

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CONCLUSIONS

Understanding the multi-facet effects of natural disturbances on temperate forest ecosystems is crucial for targeting both short- and long-term management strategies. Due to climate change, natural disturbances, such as windstorms, fires, and insect or pathogen outbreaks, will become more frequent in the future, potentially affecting carbon stocks and increasing unplanned harvests (i.e. salvage logging). Thus, a better scientific knowledge of the forest ecosystem response is needed to cope with the future challenges and to target specific management actions. The three main aims of my PhD thesis were (I) to understand the effects of large-scale disturbances across different environmental conditions, (II) to identify the role of predisposing factors in the tree susceptibility risk for large-scale insect outbreaks, and (III) to evaluate the role of post-disturbance sites as biodiversity refugia at the landscape scale.

In the first part of the thesis, I focused on wind disturbance effects on soil-living organisms, by testing interactions between forest disturbance and underlying ecological gradients. We selected three soil-related groups of organisms having different life-styles, sizes, and ecology: ground-dwelling arthropods, microarthropods, and oomycetes. First, windthrow combined with salvage logging caused mixed responses of forest communities depending on the target taxon. Soil disturbance had a negative short-term effect on ground beetles, harvestmen, springtails, and soil mites, affecting both their abundance and richness negatively. On the contrary, we found a positive effect on the diversity of spiders which are able to quickly colonise new habitats by ballooning. We also observed a slightly increase in the oomycete community diversity. Second, we found that underlying ecological gradients were also important in shaping natural communities of such soil-living organisms. Interactions between forest disturbance and underlying ecological gradients at the large spatial scale occurred for many groups of arthropods. In particular, we found that the higher impacts of wind disturbance occurred at high elevations and in historically drier sites. Finally, our findings revealed complex biotic responses to the same disturbance event, depending on the target group and the environmental conditions. When dealing with post-disturbance management of large areas, forest managers should target different strategies of restoration depending on the local conditions, especially in the protected areas with conservation purposes.

In the second part of the thesis, I studied biotic natural disturbances focusing on the predisposing factors of the outbreaks of the European spruce bark beetle (*Ips typographus* L.). The remote sensing approach allows us to study large spatial patterns of tree mortality due to the European spruce bark beetle infestations hitting the Central Europe in 2018, during a drought event. Local growing conditions of trees, as well as landscape features, were important factors for the risk of bark beetle outbreaks. Indeed, we found interactions between elevation gradient and local growing conditions of host trees. At the early stage of a large-scale outbreak, we showed that trees growing at low elevations and on flat terrains with high water availability were the most frequently attacked. Hence, future forest planning should consider the associated risk of planting pure stands of Norway spruce at low elevations, especially in high-productivity areas.

In the last part, I focused on the post-disturbance long-term response at the landscape scale. Several years after the disturbance, regeneration process converts the old wind-damaged areas in transitory habitats hosting shrubs and small trees. These mid-term succession patches are characterised by the regrowth of a dense herbaceous layer and the partial recovery of the canopy. At the landscape scale, these transition habitats co-occur with intact forest patches and managed open-habitat patches. Since the regeneration process takes many years, we used the abandonment process as proxy for studying the ecological role of temporary mid-term succession patches. Using spiders as target group, we found that temporary abandoned patches played a pivotal role in enhancing the diversity of spiders at the landscape scale. These transition habitats created by disturbance or by abandonment of managed open habitats have the potential to provide many and diverse ecological niches. Our results pointed out the importance of the forest perturbations in sustaining high biodiversity in the long terms due to higher landscape environmental heterogeneity. Forest mountain landscapes should be managed dynamically allowing small-scale and periodic disturbance regime.

Overall, two general conclusions can be derived from this thesis. First, forest disturbances are extremely complex phenomena encompassing different temporal and spatial scales, and we showed the importance of studying interactive effects. For instance, topography could play an important role in determining the impact magnitude of a large-scale windstorms on the soil-living organisms or affecting tree vulnerability to insect outbreaks. Further efforts are still needed to better understand the multifaceted effects of such phenomena, and looking at the interactions might help to fill the gap in the scientific knowledge. Second, because forest disturbance events include multiple dimensions, many complementary skills and approaches are needed. Here, I used a multidisciplinary approach integrating remote sensing, GIS science, DNA-metabarcoding and landscape ecology for studying the impact of forest disturbances. Remote sensing, molecular approaches, and landscape ecology could be implemented in the ecosystem management, together with traditional methods. The complexity of such phenomena and the variety of outcomes should be taken into consideration when implementing conservation actions for habitat restoration, carrying out salvage logging and sanitisation cuts, or planning future forest landscapes. Due to climate change these disturbances will increase in the coming years posing further challenges to the management of our forest landscapes. My PhD work contributed to emphasise the urgent need for a multidisciplinary and a holistic approach to address these challenges.

SUPPLEMENTARY MATERIALS

Chapter I

Appendix A - Collinearity of underlying environmental variables across selected sites

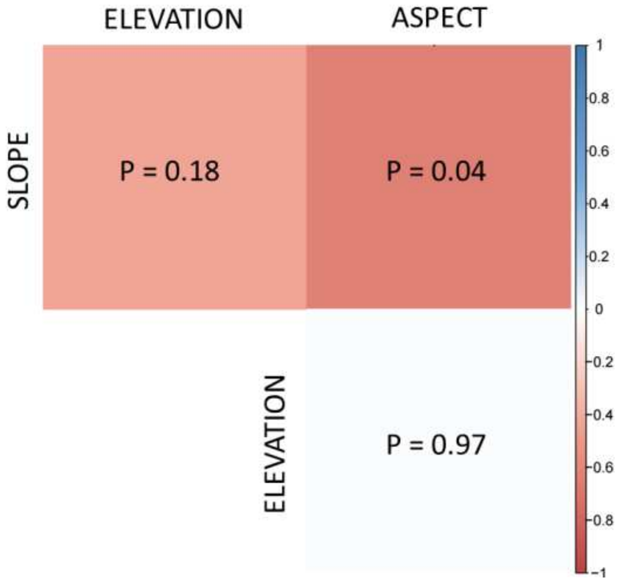


Fig. A.1 Correlations (Pearson coefficient) and relative significance between average elevation, average aspect (i.e. distance from South) and average slope across the selected sampling areas, i.e. landscapes (Correlation coefficients: elevation-slope = -0.43, elevation-aspect = 0.15, slope-aspect = -0.63; R^2: elevation-slope = 0.09, elevation-aspect = 0.00, slope-aspect = 0.33).

Appendix B - Collinearity of elevation, temperature, and ground vegetation recovery

Elevation was positively related to temperature and ground vegetation coverage. Also, temperature was higher in windfalls (temperature increasing ranged from +3°C to +4°C along elevation), as expected due to canopy removal. Here, we present collinearity relations of temperature and ground vegetation coverage in windfalls with elevation gradient.

Temperature

Temperature was assessed using 30 dataloggers (15 in forest and 15 in windfalls), covering the elevation range of our sampling. Each dataloggers was buried into the soil (about 5 cm depth) to avoid direct solar radiation. Dataloggers were protected by a 50 ml falcon tube and a plastic bag with airtight closure to prevent humidity issues. Temperature was recorder every 5 minutes. To analyze temperature trend along elevation, we computed the average temperature recorded by each datalogger during each day and then we used linear mixed models with temperature as response variable, elevation, habitat, and interaction as fixed effects, and site nested in day ID as random factor.

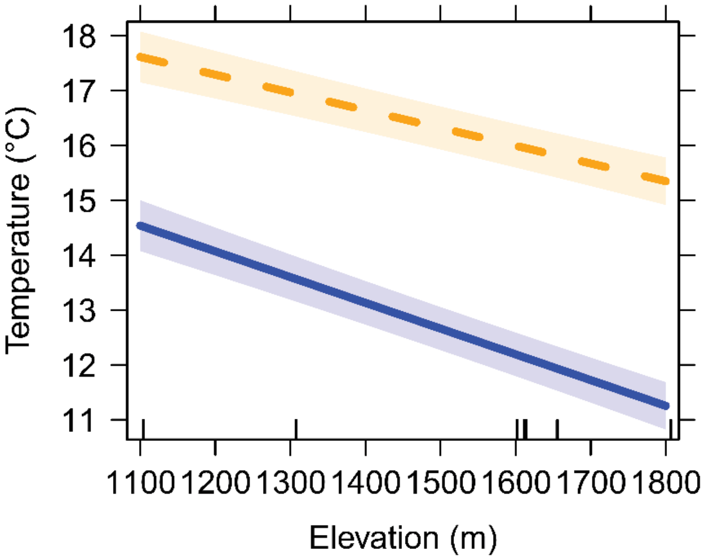


Fig. B.1 Temperature data (dataloggers) were modelled using elevation and habitat type. We recorded warmer temperature in windfalls (orange dashed line), rather than in forest (blue solid line). Moreover, decreasing with elevation was less steep in windfalls.

	Estimate	SE	df	P value
(Intercept)	1.97E+01	5.07E-01	2.18E+02	<0.001
Habitat type	1.47E+00	5.64E-01	1.25E+02	0.01010
Elevation	-4.70E-03	3.10E-04	1.93E+02	<0.001
Habitat x Elevation	1.46E-03	3.71E-04	1.25E+02	<0.001

Table B.1 Results of temperature model.

Ground vegetation coverage

Ground vegetation recovery was assessed using remote sensing data. Mean NDVI (Normalized Difference Vegetation Index) was computed during July 2020 in Google Earth Engine web platform by using Sentinel 2 images at 10 meters resolution. For each site, we polygonised logged windfalls, intact forest and meadows using QGIS software and we computed the average NDVI values. NDVI values were modelled using linear models (windfall: P value=0.008, adjusted-R^2=0.51; forest: not significant; meadow: not significant). Decreasing windfall NDVI values with increasing elevation suggests different recovery rate of the ground vegetation.

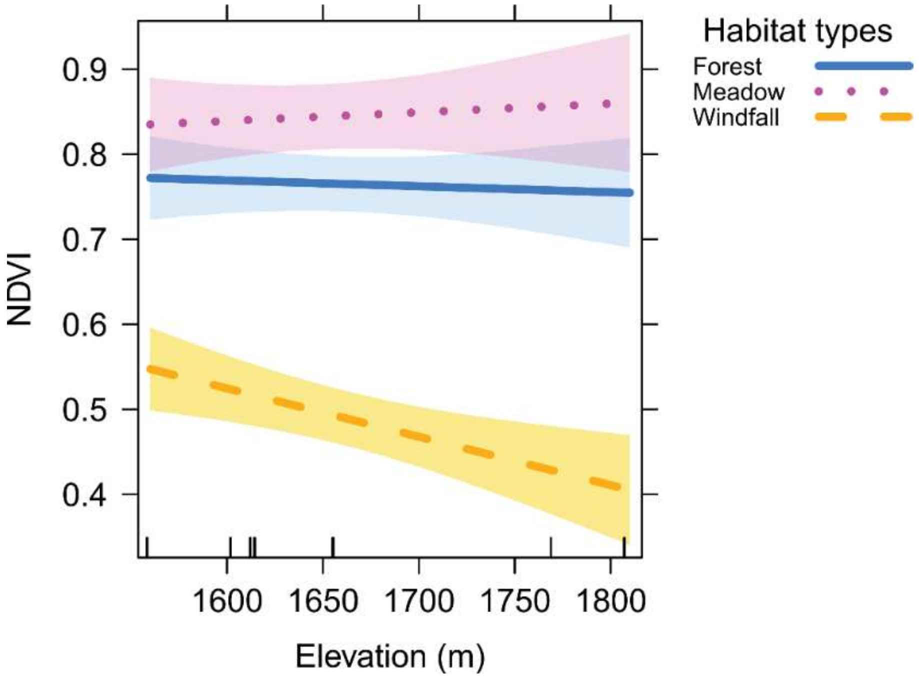


Fig. B.2 Normalized Difference Vegetation Index (NDVI) in wind disturbed areas decreased along elevation. Regression lines of NDVI values along the elevation gradient are shown for forests (blue line), meadows (pink line), and windfalls (orange line).

Appendix C - Species list with the number of individuals.

Table C.1 Species list of ground beetles (Coleoptera, Carabidae)

Family	Species	Individuals
Carabidae	*Abax parallelepipedus* (Piller & Mitterpacher, 1783)	30
Carabidae	*Abax pilleri* Csiki, 1916	564
Carabidae	*Agonum sexpunctatum* (Linnaeus, 1758)	8
Carabidae	*Agonum viduum* (Panzer, 1796)	1
Carabidae	*Amara erratica* (Duftschmid, 1812)	1
Carabidae	*Amara montivaga* Sturm, 1825	17
Carabidae	*Bembidion incognitum* G.Müller, 1931	11
Carabidae	*Bembidion lampros* (Herbst, 1784)	8
Carabidae	*Calathus micropterus* (Duftschmid, 1812)	157
Carabidae	*Carabus auronitens* Fabricius, 1792	16
Carabidae	*Carabus convexus* Fabricius, 1775	5
Carabidae	*Carabus germarii* Sturm, 1815	180
Carabidae	*Carabus hortensis* Linnaeus, 1758	10
Carabidae	*Carabus linnaei* Panzer, 1812	250
Carabidae	*Cychrus attenuatus* (Fabricius, 1792)	21
Carabidae	*Cychrus caraboides* (Linnaeus, 1758)	1
Carabidae	*Dromius agilis* (Fabricius, 1787)	1
Carabidae	*Harpalus laevipes* Zetterstedt, 1828	41
Carabidae	*Leistus nitidus* (Duftschmid, 1812)	12
Carabidae	*Limodromus assimilis* (Paykull, 1790)	1
Carabidae	*Loricera pilicornis* (Fabricius, 1775)	1
Carabidae	*Molops piceus* (Panzer, 1793)	7
Carabidae	*Notiophilus biguttatus* (Fabricius, 1779)	91
Carabidae	*Platyderus rufus* (Duftschmid, 1812)	1
Carabidae	*Poecilus versicolor* (Sturm, 1824)	1
Carabidae	*Pterostichus (Cheporus) burmeisteri* Heer, 1837	918
Carabidae	*Pterostichus (Oreophilus) jurinei* (Panzer, 1802)	852
Carabidae	*Pterostichus* sp. 1	1
Carabidae	*Pterostichus oblongopunctatus* (Fabricius, 1787)	23
Carabidae	*Pterostichus unctulatus* (Duftschmid, 1812)	1167
Carabidae	*Trichotichnus laevicollis* (Duftschmid, 1812)	4

Table C.2 species list of spiders (Araneae).

Note: males of *Pardosa alacris* and *Pardosa lugubris* were distinguished here, but females are pooled in the species group level (i.e. *Pardosa* gr. *lugubris*) because they cannot be easily distinguished. In statistical analyses we used the species group level identification.

Family	Species	Adults
Agelenidae	*Coelotes mediocris* Kulczynski, 1887	20
Agelenidae	*Histopona torpida* (C. L. Koch, 1837)	164
Agelenidae	*Inermocoelotes inermis* (L. Koch, 1855)	6
Agelenidae	*Tegenaria mirifica* Thaler, 1987	2
Agelenidae	*Tegenaria silvestris* L. Koch, 1872	7
Amaurobiidae	*Amaurobius obustus* L. Koch, 1868	19
Amaurobiidae	*Callobius claustrarius* (Hahn, 1833)	14
Araneidae	*Gibbaranea omoeda* (Thorell, 1870)	2
Clubionidae	*Clubiona saxatilis* L. Koch, 1867	1
Clubionidae	*Clubiona subsultans* Thorell, 1875	4
Clubionidae	*Clubiona terrestris* Westring, 1851	3
Cybaeidae	*Cryphoeca silvicola* (C. L. Koch, 1835)	26
Cybaeidae	*Cybaeus tetricus* (C. L. Koch, 1839)	353
Dysderidae	*Dasumia canestrinii* (Thorell, 1871)	1
Gnaphosidae	*Drassodes pubescens* (L. Koch, 1876)	22
Gnaphosidae	*Drassyllus pusillus* (Thorell, 1856)	1
Gnaphosidae	*Gnaphosa badia* (C. L. Koch, 1833)	9
Gnaphosidae	*Haplodrassus signifer* (L. Koch, 1866)	23
Gnaphosidae	*Haplodrassus silvestris* (C. L. Koch, 1839)	5
Gnaphosidae	*Haplodrassus soerenseni* (Blackwall, 1833)	9
Gnaphosidae	*Micaria aenea* (Strand, 1900)	13
Gnaphosidae	*Micaria fulgens* Thorell, 1871	13
Gnaphosidae	*Micaria pulicaria* (Walckenaer, 1802)	1
Gnaphosidae	*Zelotes clivicola* (Sundevall, 1831)	18
Gnaphosidae	*Zelotes erebeus* (L. Koch, 1870)	5
Gnaphosidae	*Zelotes subterraneus* (Thorell, 1871)	57
Hahniidae	*Mastigusa arietina* (C. L. Koch, 1833)	3
Linyphiidae	*Agyneta affinis* (L. Koch, 1872)	2
Linyphiidae	*Agyneta conigera* (O. Pickard-Cambridge, 1875)	33
Linyphiidae	*Agyneta ramosa* (Kulczynski, 1887)	2
Linyphiidae	*Agyneta rurestris* Lessert, 1907	51
Linyphiidae	*Anguliphantes monticola* (Wider, 1834)	2
Linyphiidae	*Asthenargus paganus* (Blackwall, 1834)	17
Linyphiidae	*Asthenargus perforatus* (O. Pickard-Cambridge, 1873)	1
Linyphiidae	*Caracladus avicula* (O. Pickard-Cambridge, 1863)	18
Linyphiidae	*Centromerus brevipalpus* (Wider, 1834)	1
Linyphiidae	*Centromerus cavernarum* Blackwall, 1833	3
Linyphiidae	*Centromerus pabulator* Emerton, 1882	10
Linyphiidae	*Centromerus silvicola* (Wider, 1834)	2
Linyphiidae	*Centromerus* sp. 1	1

Linyphiidae	*Centromerus subalpinus* O. Pickard-Cambridge, 1872	2
Linyphiidae	*Ceratinella brevis* (O. Pickard-Cambridge, 1871)	14
Linyphiidae	*Dicymbium nigrum* (Thorell, 1875)	2
Linyphiidae	*Diplocephalus alpinus* Simon, 1884	6
Linyphiidae	*Diplocephalus latifrons* (Wider, 1834)	308
Linyphiidae	*Diplostyla concolor* (Wunderlich, 1985)	60
Linyphiidae	*Erigone atra* (O. Pickard-Cambridge, 1873)	3
Linyphiidae	*Erigone autumnalis* (Emerton, 1882)	1
Linyphiidae	*Erigone dentipalpis* (O. Pickard-Cambridge, 1871)	15
Linyphiidae	*Gongylidiellum latebricola* (Wider, 1834)	2
Linyphiidae	*Improphantes nitidus* (Wider, 1834)	1
Linyphiidae	*Lepthyphantes nodifer* (Kulczynski, 1898)	5
Linyphiidae	*Macrargus rufus* (O. Pickard-Cambridge, 1871)	7
Linyphiidae	*Mansuphantes pseudoarciger* (Wider, 1834)	2
Linyphiidae	*Mecopisthes silus* (L. Koch, 1872)	10
Linyphiidae	*Mermessus trilobatus* (C. L. Koch, 1836)	5
Linyphiidae	*Micrargus apertus* F. O. Pickard-Cambridge, 1894	1
Linyphiidae	*Micrargus* gr. *herbigradus*	11
Linyphiidae	*Microneta viaria* (O. Pickard-Cambridge, 1906)	2
Linyphiidae	*Minyriolus pusillus* Simon, 1913	4
Linyphiidae	*Neriene peltata* Lessert, 1907	1
Linyphiidae	*Palliduphantes* cf. *antroniensis*	1
Linyphiidae	*Palliduphantes montanus* Millidge, 1979	7
Linyphiidae	*Palliduphantes pallidus* Millidge, 1979	1
Linyphiidae	*Pelecopsis elongata* (O. Pickard-Cambridge, 1873)	3
Linyphiidae	*Pelecopsis radicicola* (Blackwall, 1853)	44
Linyphiidae	*Pityohyphantes phrygianus* (Wider, 1834)	5
Linyphiidae	*Porrhomma campbelli* (O. Pickard-Cambridge, 1878)	1
Linyphiidae	*Porrhomma* cf. *pallidum*	3
Linyphiidae	*Saaristoa firma* Blackwall, 1833	3
Linyphiidae	*Scotargus pilosus* (Crosby & Bishop, 1931)	5
Linyphiidae	*Tapinocyba affinis* Chyzer & Kulczynski, 1894	29
Linyphiidae	*Tapinocyba pallens* (Blackwall, 1833)	19
Linyphiidae	*Tenuiphantes alacris* (C. L. Koch, 1835)	131
Linyphiidae	*Tenuiphantes tenebricola* (Simon, 1876)	177
Linyphiidae	*Troglohyphantes* gr. *lucifuga*	3
Linyphiidae	*Walckenaeria atrotibialis* (Walckenaer, 1805)	2
Linyphiidae	*Walckenaeria cuspidata* (Latreille, 1817)	1
Linyphiidae	*Walckenaeria furcillata* (Clerck, 1757)	1
Linyphiidae	*Walckenaeria obtusa* (C. L. Koch, 1834)	4
Liocranidae	*Agroeca brunnea* (C. L. Koch, 1833)	1
Lycosidae	*Alopecosa taeniata* (L. Koch, 1870)	178
Lycosidae	*Arctosa lutetiana* (Walckenaer, 1802)	2
Lycosidae	*Aulonia albimana* (Linnaeus, 1758)	4
Lycosidae	*Hogna radiata* (C. L. Koch, 1833)	1

Lycosidae	*Pardosa alacris* (C. L. Koch, 1834) (only males, as females cannot be distinguished from *Pardosa lugubris* (Kulczynski, 1881))	6
Lycosidae	*Pardosa amentata* (Kulczynski, 1898)	2
Lycosidae	*Pardosa bifasciata* (O. Pickard-Cambridge, 1863)	1
Lycosidae	*Pardosa blanda* Jackson, 1912	26
Lycosidae	*Pardosa* cf. *oreophila*	1
Lycosidae	*Pardosa ferruginea* (C. L. Koch, 1836)	1085
Lycosidae	*Pardosa* gr. *lugubris* (only females)	252
Lycosidae	*Pardosa lugubris* (Kulczynski, 1881) (only males, as females cannot be distinguished from *Pardosa alacris* (C. L. Koch, 1834))	399
Lycosidae	*Pardosa palustris* (Simon, 1884)	7
Lycosidae	*Pardosa riparia* Schenkel, 1929	593
Lycosidae	*Pardosa sordidata* (L. Koch, 1869)	22
Lycosidae	*Trochosa* sp. (females)	27
Lycosidae	*Xerolycosa nemoralis* (Menge, 1866)	35
Miturgidae	*Zora nemoralis* (Westring, 1861)	23
Miturgidae	*Zora spinimana* C. L. Koch, 1835	1
Philodromidae	*Philodromus collinus* (Clerck, 1757)	4
Philodromidae	*Philodromus margaritatus* Simon, 1875	1
Philodromidae	*Philodromus vagulus* (Clerck, 1757)	1
Phrurolithidae	*Phrurolithus festivus* (Walckenaer, 1802)	7
Pisauridae	*Pisaura mirabilis* (Blackwall, 1853)	4
Salticidae	*Euophrys frontalis* (Walckenaer, 1826)	2
Salticidae	*Neon reticulatus* (C. L. Koch, 1846)	1
Salticidae	*Pseudeuophrys erratica* (Linnaeus, 1758)	1
Salticidae	*Sittisax saxicola* Gétaz, 1889	1
Segestriidae	*Segestria senoculata* (Clerck, 1757)	8
Theridiidae	*Enoplognatha ovata* (Blackwall, 1846)	1
Theridiidae	*Robertus truncorum* (Schrank, 1803)	40
Thomisidae	*Ozyptila trux* Simon, 1932	2
Thomisidae	*Xysticus audax* C. L. Koch, 1837	10
Thomisidae	*Xysticus bifasciatus* C. L. Koch, 1835	1
Thomisidae	*Xysticus cristatus* (Blackwall, 1861)	3
Thomisidae	*Xysticus lanio* (Sundevall, 1833)	1

Fig. C.3 Species list of harvestmen (Opiliones)

Family	**Species**	**Individuals**
Nemastomatidae	*Histricostoma* cf. *dentipalpe*	238
Nemastomatidae	*Mitostoma* cf. *chrysomelas*	91
Nemastomatidae	*Nemastoma* cf. *dentigerum*	2
Nemastomatidae	*Paranemastoma* cf. *quadripunctatum*	88
Phalangiidae	*Amilenus* cf. *aurianticus*	35
Phalangiidae	*Mitopus* cf. *morio*	2767
Phalangiidae	*Oligolophus* cf. *tridens*	1
Phalangiidae	*Phalangium* cf. *opilio*	88
Phalangiidae	*Platybunus* cf. *pinetorum*	175
Phalangiidae	*Rilaena* cf. *triangularis*	4
Sclerosomatidae	*Astrobunus* cf. *helleri*	29
Trogulidae	*Anelasmocephalus sp.*	4
Trogulidae	*Trogulus sp.*	70

Chapter II

Appendix A – taxonomic resolution OTU

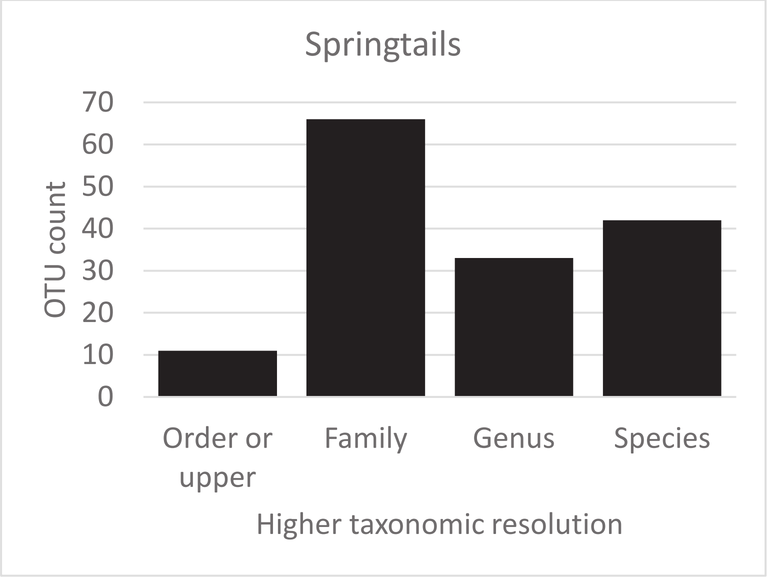


Figure A.1 – Taxonomic resolution achievable for springtail OTUs

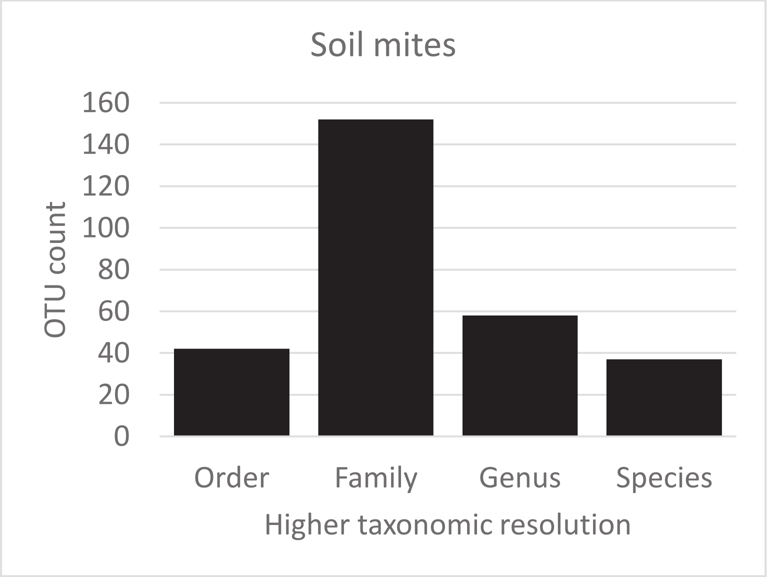


Figure A.2 – Taxonomic resolution achievable for soil mite OTUs

Appendix B - Moss cover

For each subplot (pseudo-replicates), we visually estimated moss coverage. Then, for each sampling point the average value was computed and used as environmental variable (expressed as percentage). We tested moss cover loss between forest and windfall using linear mixed effect models (package lme4 in R). We used moss cover as response variable, habitat as explanatory variable, and pair ID as random effect. We found that moss cover was overall reduced in windfalls (P value < 0.0001).

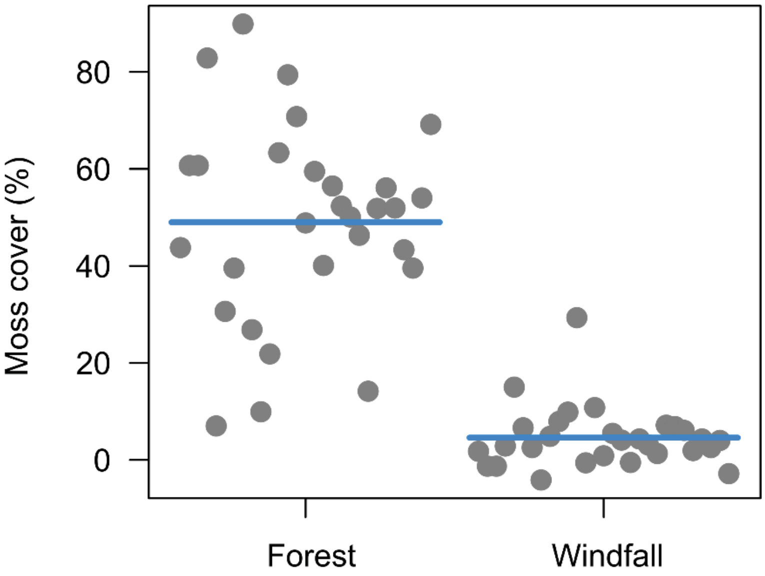


Fig B.1 Moss cover loss due to habitat change (windstorm disturbance).

Chapter IV

Appendix A: Remote sensing information for bark beetle infestation detection.

Tile code	2018	2019
T32UMV	2018-02-24	2019-03-21
T32ULV	2018-02-24	2019-03-21
T32UMU	2018-02-24	2019-03-31
T32TLT	2018-03-24 and 2017-11-01	2019-03-21
T32ULU	2018-03-24 and 2018-04-20	2019-03-21
T31UER	2018-02-25	2019-04-01
T31UEQ	2018-02-25	2019-03-22
T31UEP	2018-02-25	2019-03-22
T31TEN	2018-02-25 and 2018-03-24	2019-03-22
T31TEM	2018-02-27 and 2018-03-14	2019-02-27
T31TFM	2018-02-27	2019-03-24
T31TFN	2018-03-24	2019-03-29
T31UFP	2018-02-22	2019-02-27
T31UFQ	2018-02-22	2019-02-27
T31UFR	2018-03-24	2019-02-27
T31UGQ	2018-02-22	2019-02-27
T31UGP	2018-03-24	2019-02-27
T31TGN	2018-03-24	2019-03-21
T31TGM	2018-03-24	2019-03-31

Table A.1: Sentinel 2 tiles employed in bark beetle detection are listed. Date of acquisition is shown in YYYY-MM-DD format.

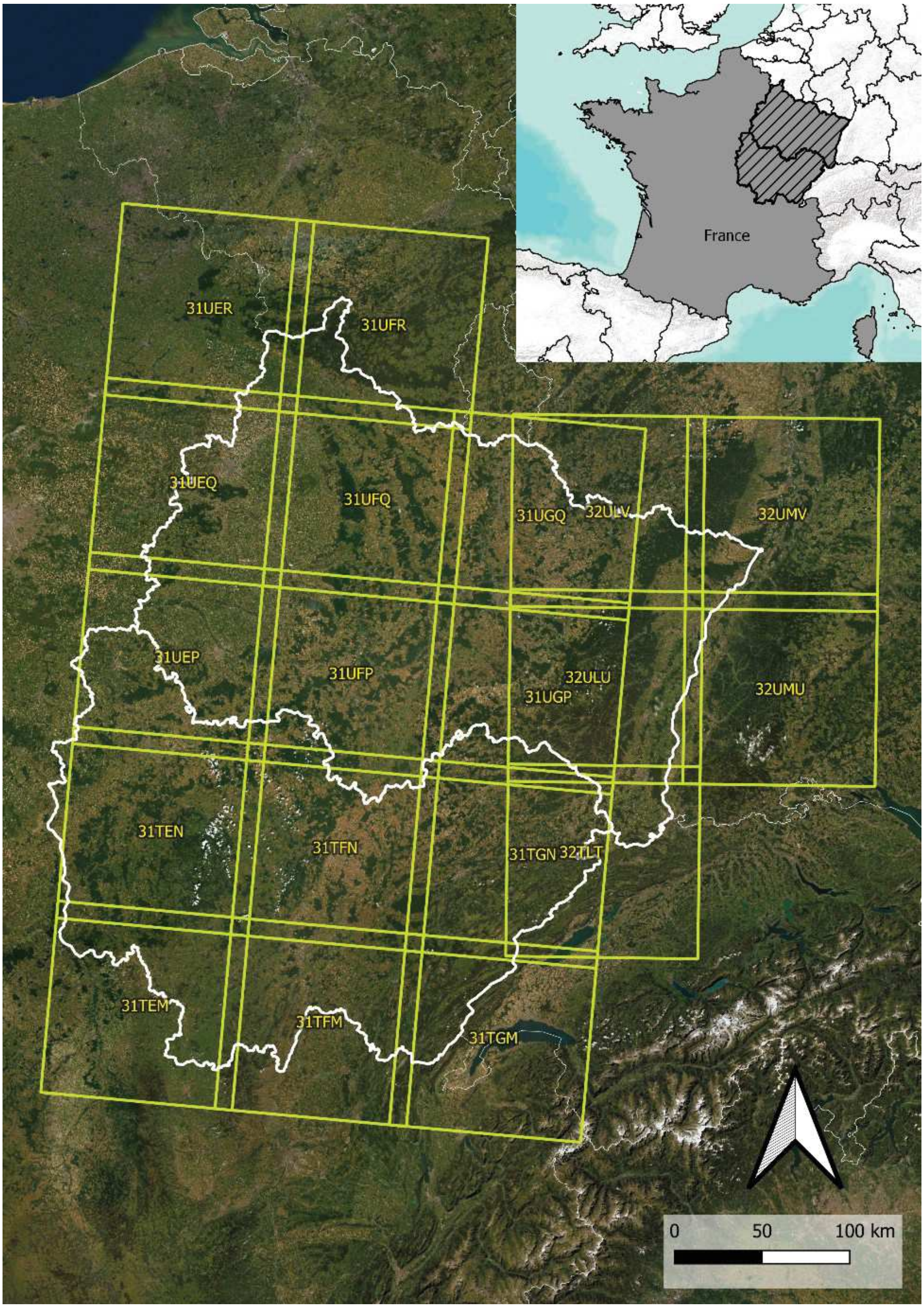


Fig. A.1: Sentinel 2 tiles used in the study. Each tile was cropped over study area.

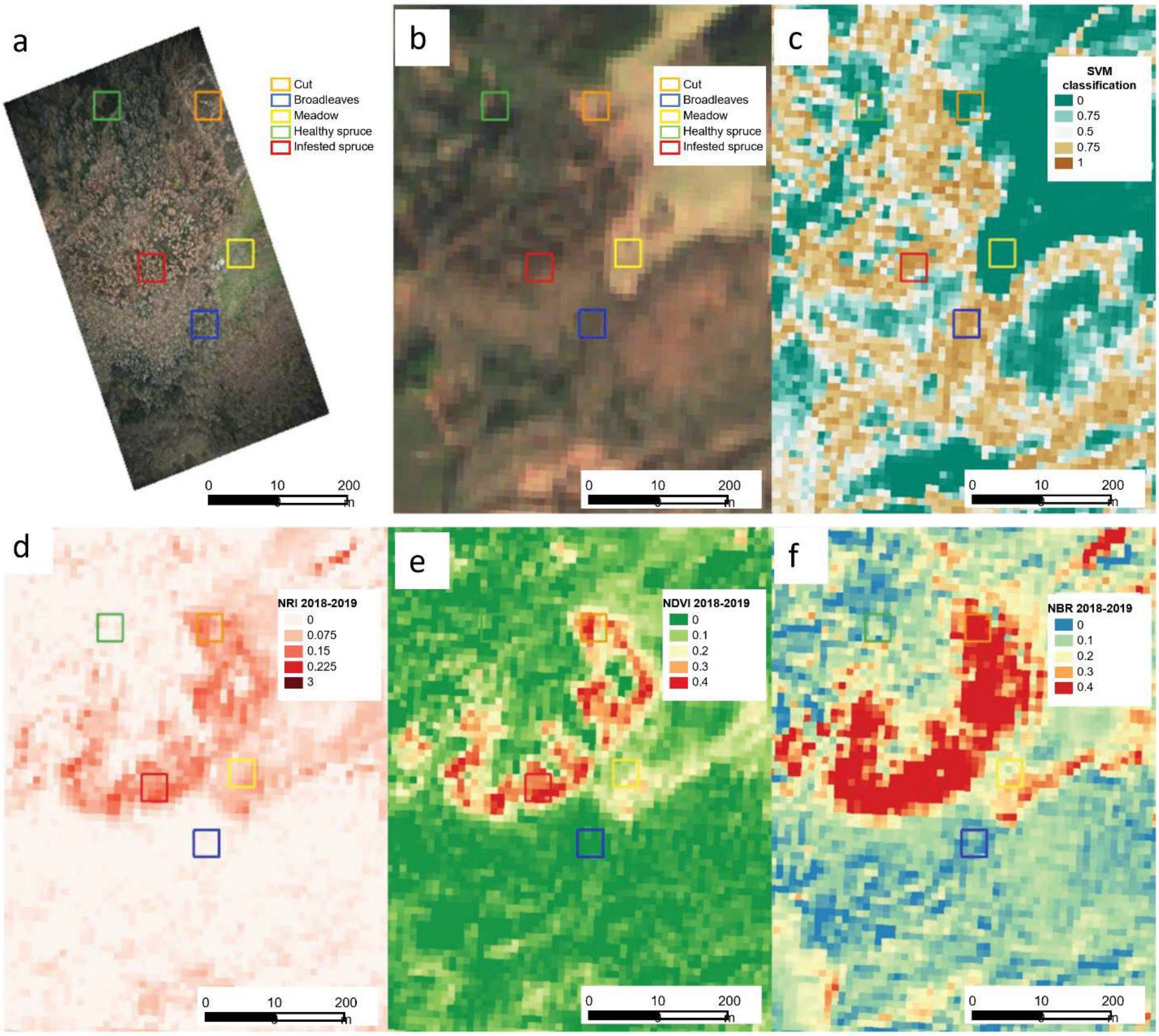
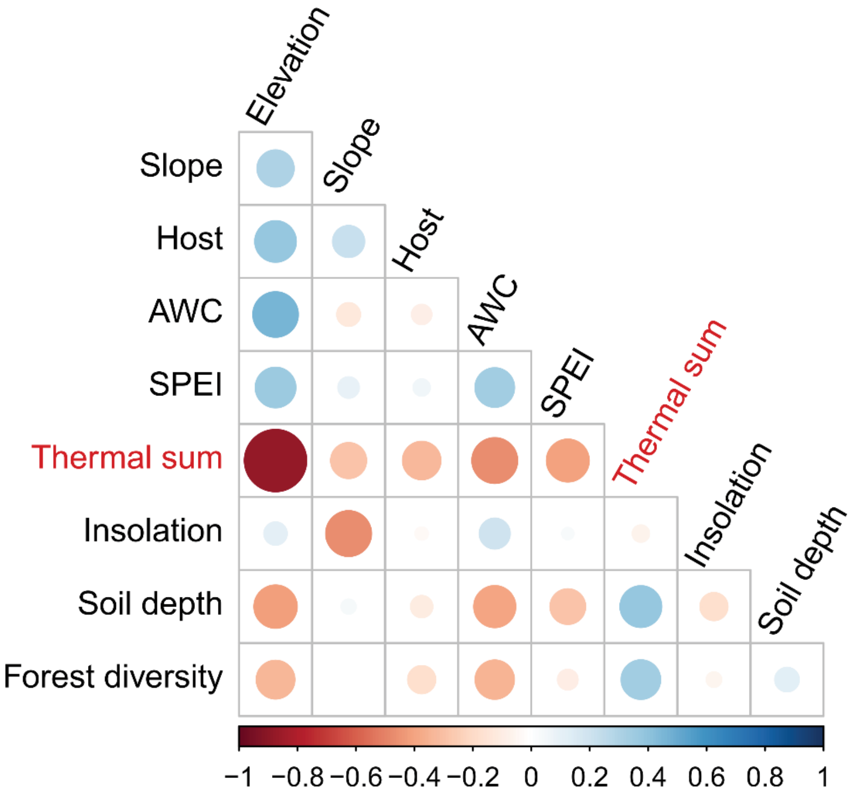


Fig. A.2 Comparison of high resolution images from aerial survey (a) with multispectral layers from Sentinel 2: real colours (b), SVM classification (c), NRI index (d), NDVI index (e), and NBR index (f). Five types of land use are shown: cut (orange), broadleaves forest (blue), meadow (yellow), healthy spruce forest (green), and infested spruce forest (red).

		Model			
		Damaged pixels	Not damaged pixels	Recall	False negatives
Ground truth data	Damaged pixels	647	252	0.72	28%
	Not damaged pixels	205	7866	0.97	2.50%
	Accuracy	0.76	0.97		
	False positives	24.10%	3.10%		
	Kappa	**0.71**			
	Overall Accuracy	**94.90%**			

Table A.2: Confusion matrix of bark beetle detection method. Ground truth data is referring to the high resolution aerial images (5 cm resolution), which has been used to categorize satellite pixels (10 metres of resolution).

Appendix B: Statistical supplementary materials – Models



	Elevation	**Slope**	**Host**	**AWC**	**SPEI**	**Thermal sum**	**Insolation**	**Soil depth**
Slope	0.31							
Host	0.38	0.23						
AWC	0.46	-0.12	-0.09					
SPEI	0.37	0.1	0.06	0.35				
Thermal Sum	-0.87	-0.29	-0.33	-0.47	-0.41			
Insolation	0.12	-0.47	-0.04	0.21	0.03	-0.06		
Soil depth	-0.42	0.05	-0.11	-0.39	-0.28	0.39	-0.17	
Forest diversity	-0.33	-0.02	-0.17	-0.34	-0.09	0.35	-0.05	0.13

Table-Figure B.1 Pearson correlation coefficients for covariates. Significative correlations are shown in Figure B.1 and relative Table B.1. Thermal sum was excluded by models due to high correlation with the elevation.

Variables	*Estimate*	*Adjusted S.E.*	*Z value*	*P value*
Intercept	**-1.945**	**0.042**	**46.445**	**<0.0001**
RAC	**1.699**	**0.060**	**28.375**	**<0.0001**
Elevation	**-1.715**	**0.113**	**15.119**	**<0.0001**
Host	**0.728**	**0.080**	**9.076**	**<0.0001**
Forest diversity	**-0.325**	**0.061**	**5.318**	**<0.0001**
SPEI	**-0.437**	**0.110**	**3.982**	**<0.0001**
Insolation	0.054	0.081	0.668	0.504
Slope	**-0.499**	**0.091**	**5.499**	**<0.0001**
AWC	**0.200**	**0.093**	**2.151**	**0.032**
Soil depth	-0.072	0.080	0.901	0.367
Elevation x SPEI	-0.427	0.252	1.695	0.090
Elevation x Insolation	0.251	0.255	0.983	0.326
Elevation x Slope	**0.753**	**0.197**	**3.817**	**<0.001**
Elevation x AWC	**-0.878**	**0.177**	**4.960**	**<0.0001**
Elevation x Soil depth	0.069	0.143	0.483	0.629
SPEI x Insolation	0.008	0.079	0.095	0.924
SPEI x Slope	0.026	0.107	0.239	0.811
SPEI x AWC	0.003	0.075	0.045	0.965
SPEI x Soil depth	**0.388**	**0.132**	**2.940**	**0.003**

Table B.2 Summary of 1 km grid model with occurrence data

Chapter V

Appendix A

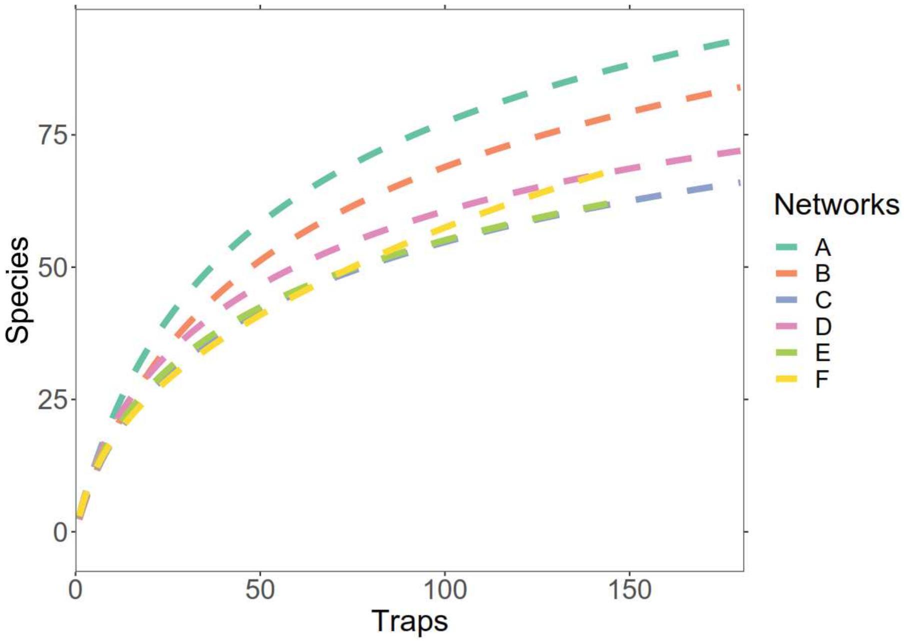


Fig. A.1 Accumulation curves of species richness on number of traps. Data are aggregated by landscape ID.

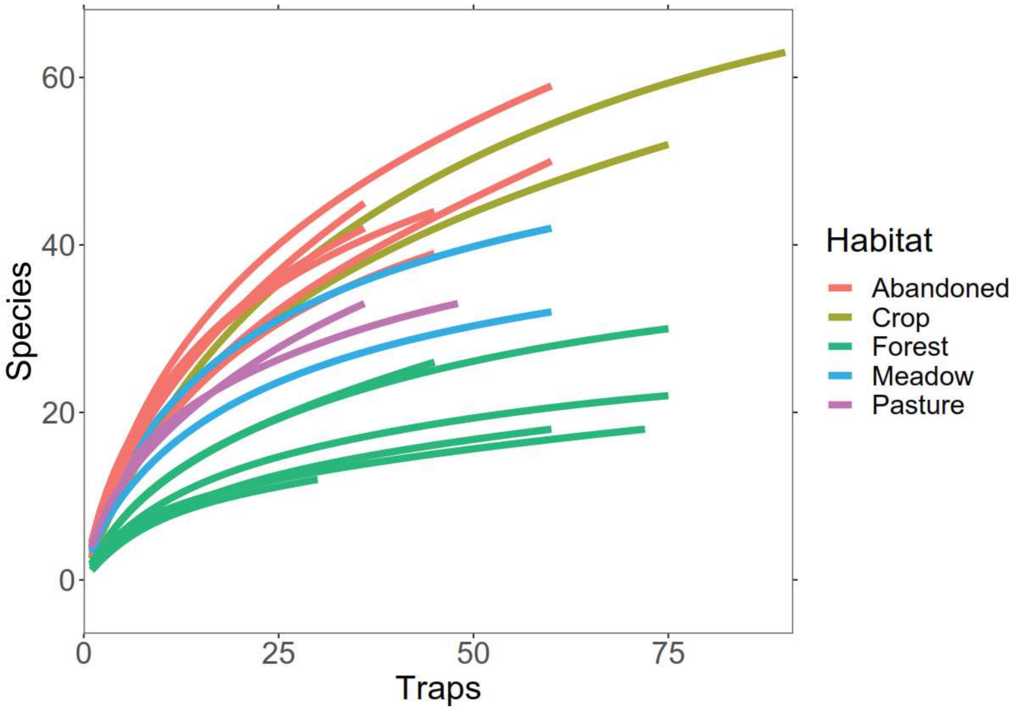


Fig. A.2 Accumulation curves showing the species richness on number of traps. Data are aggregated by same habitat nested in each landscape.

Appendix B

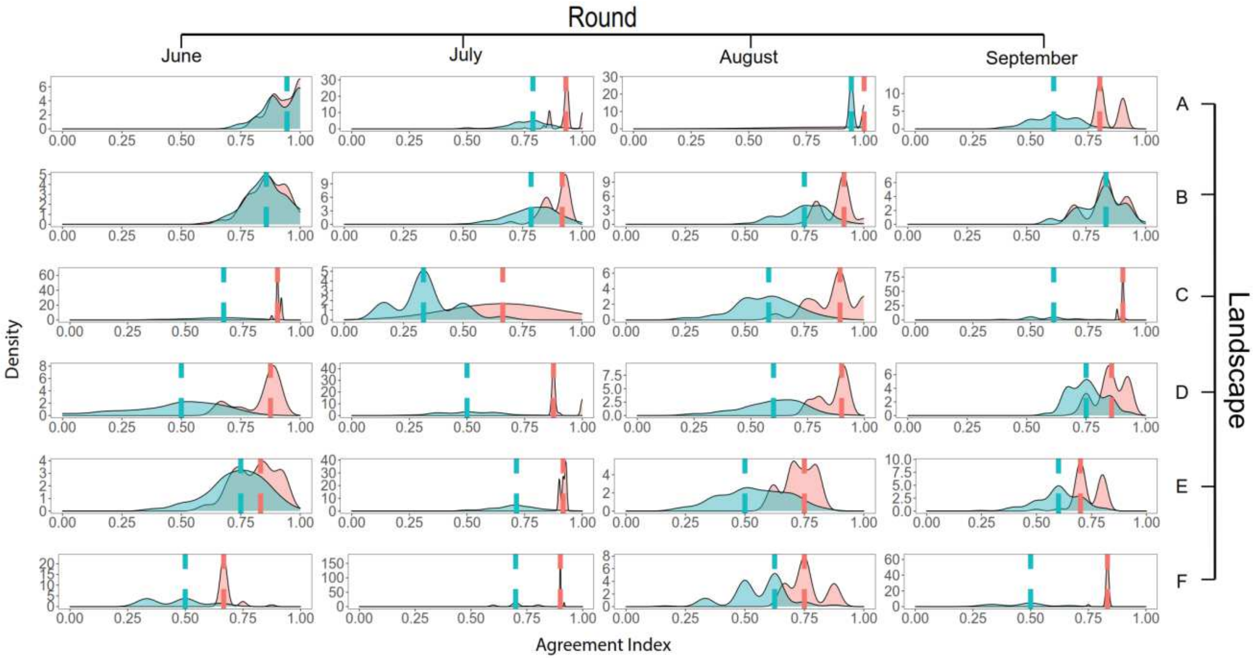


Fig. B.1 For each landscape and round, the density distributions of observed Agreement index (red) and null Agreement index (blue) are shown. Dashed lines represent medians of the two distributions. Observed values of the agreement index are generally higher than null models. Agreement index (Lami et al., 2020) aims to quantify the intra-module habitat diversity, ranging from 0 (each module contains all habitats) to 1 (each module contains only patches belonging to the same habitat). Since different networks can take different value distributions depending on the number and label within each one, the observed pattern needs to be compared with a null model in order to assess the outcomes. In details, each computed module arrangement was compared with a permutation of habitat labels (null models). We reiterated the process for 100 times.

Reference

Lami, F., Bartomeus, I., Nardi, D., Beduschi, T., Boscutti, F., Pantini, P., Santoiemma, G., Scherber, C., Tscharntke, T., Marini, L., 2021. Species–habitat networks elucidate landscape effects on habitat specialisation of natural enemies and pollinators. Ecol. Lett. 24, 288–297. https://doi.org/10.1111/ele.1364

Appendix C

Table C.1: List of the species and their total abundance in the different habitats across all investigated landscape.

Families	**Species**	**Habitat**									Notes
		Abandoned			**Forest**			**Crop**	**Meadow**	**Pasture**	
		Low-belt	**Medium-belt**	**High-belt**	**Low-belt**	**Medium-belt**	**High-belt**	**Low-belt**	**Medium-belt**	**High-belt**	
Agelenidae		2	4	13	21	270	363	4	1	2	
	Agelena labyrinthica (Clerck, 1757)	1									
	Coelotes mediocris Kulczynski, 1887			5			150			1	
	Eratigena agrestis (Walckenaer, 1802)							1			
	Histopona torpida (C.L. Koch, 1837)		2	6	12	248	194				
	Inermocoelotes microlepidus (De Blauwe, 1973)					12	1				
	Tegenaria hasperi Chyzer, 1897	1			1			3			
	Tegenaria silvestris L. Koch, 1872		2	2	1	10	18		1	1	
	Textrix caudata L. Koch, 1872				4						
	Textrix pinicola Simon, 1875				3						*sensu* Thaler Noflatcher 1990
Amaurobiidae			1	3	8	35	13				
	Amaurobius jugorum L. Koch, 1868		1	2	8	33					
	Amaurobius ruffoi Thaler, 1990			1		2	13				
Anyphaenidae						2					
	Anyphaena accentuata (Walckenaer, 1802)					2					

Atypidae			7	10		10				1	
	Atypus piceus (Sulzer, 1776)		7	10		10				1	
Cheiracanthiidae									1		
	Cheiracanthium virescens (Sundevall, 1833)								1		
Clubionidae				3	1	1	4	1	1		
	Clubiona comta C.L. Koch, 1839						1				
	Clubiona neglecta O. P.-Cambridge, 1862			1				1	1		
	Clubiona reclusa O. P.-Cambridge, 1863			2			2				
	Clubiona terrestris Westring, 1851				1	1	1				
Cybaeidae			4	7		40	15		1		
	Cybaeus minor Chyzer, 1897		4	7		40	15		1		
Dictynidae		17	1					13	6		
	Argenna subnigra (O. P.-Cambridge, 1861)	17	1					13	6		
Dysderidae		6	12	3	22	35	7	5	7		
	Dasumia canestrinii (L. Koch, 1876)	4	2		16	12					
	Dysdera crocata C.L. Koch, 1838	1						1			
	Dysdera sp.	1						2			(adult females) *D.* cf. *kollari*
	Dysdera ninnii Canestrini, 1868		10	3	6	22	3	2	5		
	Dysdera pristiphora Pesarini, 2001					1	4		2		
Gnaphosidae		195	72	83	24	1	1	174	91	53	
	Callilepis schuszteri (Herman, 1879)				1			2			
	Civizelotes pygmaeus (Miller, 1943)	1									

Drassodes lapidosus (Walckenaer, 1802)	2						2		1	
Drassodes pubescens (Thorell, 1856)			21					1	3	
Drassyllus praeficus (L. Koch, 1866)	37		3					3	17	
Drassyllus pumilus (C.L. Koch, 1839)			14				23	13		
Drassyllus pusillus (C.L. Koch, 1833)	2		16			1	7	34	13	
Drassyllus villicus (Thorell, 1875)	12	1	1	18	1		5			
Haplodrassus dalmatensis (L. Koch, 1866)	14						27		1	
Haplodrassus kulczynskii Lohmander, 1942							2	3		
Haplodrassus signifer (C.L. Koch, 1839)	5	2	5				3	5	2	
Micaria albovittata (Lucas, 1846)								12		
Micaria fulgens (Walckenaer, 1802)			4							
Micaria pulicaria (Sundevall, 1831)			7					5		
Nomisia exornata (C.L. Koch, 1839)	13						2			
Phaeocedus braccatus (L. Koch, 1866)	9						3			
Scotophaeus scutulatus (L. Koch, 1866)				1						
Marinarozelotes mutabilis (Simon, 1878)	25						1			
Trachyzelotes pedestris (C.L. Koch, 1837)	3	5	1				1			
Zelotes aeneus (Simon, 1878)	9	9					25			
Zelotes apricorum (L. Koch, 1876)		3		3						
Zelotes atrocaeruleus (Simon, 1878)	7						8			
Zelotes erebeus (Thorell, 1871)	3	14	1	1			4			

	Zelotes hermani (Chyzer, 1897)	34	3					51	2		
	Zelotes latreillei (Simon, 1878)		35	6					13	16	
	Zelotes sp A							10			Probably a new species (males and females)
	Zelotes oblongus (C.L. Koch, 1833)	18									
	Zelotes petrensis (C.L. Koch, 1839)			2							
	Zelotes subterraneus (C.L. Koch, 1833)			2							
	Zelotes tenuis (L. Koch, 1866)	1						2			
Hahniidae				31				2	7		
	Hahnia pusilla C.L. Koch, 1841			31				2	7		
Linyphiidae		34	27	74	12	46	56	133	57	137	
	Agyneta rurestris (C.L. Koch, 1836)	6	3					45	20	5	Few individuals have been determined as *A*. cf. *rurestris*
	Bathyphantes gracilis (Blackwall, 1841)						1				
	Bolyphantes kolosvaryi (Di Caporiacco, 1936)			1						1	
	Centromerus tongiorgii Ballarin & Pantini, 2020					1					
	Ceratinella brevipes (Westring, 1851)							10		1	
	Ceratinella brevis (Wider, 1834)			7						13	
	Dicymbium nigrum (Blackwall, 1834)			1		1			7		
	Diplocephalus latifrons (O. P.-Cambridge, 1863)						4				
	Diplostyla concolor (Wider, 1834)	1	2	2		3	1	15	3		
	Erigone autumnalis Emerton, 1882	1			1			5	3		

Erigone dentipalpis (Wider, 1834)							6	7	5	
Frontinellina frutetorum (C.L. Koch, 1834)	1									
Gonatium paradoxum (L. Koch, 1869)			1							
Gonatium rubellum (Blackwall, 1841)			1							
Gongylidiellum latebricola (O. Pickard-Cambridge, 1871)			6						5	
Ipa keyserlingi (Ausserer, 1867)	6						9			
Lasiargus hirsutus (Menge, 1869)	1						1			
Leptorhoptrum robustum (Westring, 1851)									1	
Mecopisthes silus (O. P.-Cambridge, 1872)		3								
Mermessus trilobatus (Emerton, 1882)	1						7	3	11	
Metopobactrus prominulus (O. P.-Cambridge, 1872)							1			
Micrargus herbigradus (Blackwall, 1854)			1		4	2				
Micrargus subaequalis (Westring, 1851)			2							
Microctenonyx subitaneus (O. P.-Cambridge, 1875)	3						2			
Microneta viaria (Blackwall, 1841)			1		6	3				
Nematogmus sanguinolentus (Walckenaer, 1842)		2						4		
Oedothorax retusus (Westring, 1851)								1		
Palliduphantes pallidus (O. P.-Cambridge, 1871)								1		
Panamomops inconspicuus (Miller & Valesova, 1964)						1				
Pelecopsis parallela (Wider, 1834)							11			

	Pelecopsis radicicola (L. Koch, 1872)			7						1	
	Pocadicnemis pumila (Blackwall, 1841)			2						2	
	Porrhomma microphthalmum (O. P.-Cambridge, 1871)					1					
	Sintula corniger (Blackwall, 1856)			2							
	Tenuiphantes flavipes (Blackwall, 1854)		1		9	22					
	Tenuiphantes tenebricola (Wider, 1834)		5			2	27				
	Tenuiphantes tenuis (Blackwall, 1852)	4	11	37		4	16	21	7	75	
	Theonina cornix (Simon, 1881)	1				1					
	Thyreosthenius parasiticus (Westring, 1851)									1	
	Tiso vagans (Blackwall, 1834)			1						13	
	Trichoncus hackmani Millidge, 1955	9			2				1		Few individuals have been determined as *T.* cf. *hackmani*
	Troglohyphantes ruffoi Di Caporiacco, 1936					1	1				
	Walckenaeria acuminata Blackwall, 1833			1							
	Walckenaeria antica (Wider, 1834)									3	
	Walckenaeria furcillata (Menge, 1869)			1							
Liocranidae		3	7	3	9	5		4			
	Agraecina lineata (Simon, 1878)	3						1			
	Agroeca brunnea (Blackwall, 1833)		1					1			
	Agroeca cuprea Menge, 1873		6			4					
	Agroeca lusatica (L. Koch, 1875)							2			

	Agroeca proxima (O. P.-Cambridge, 1871)			3							
	Liocranum rupicola (Walckenaer, 1830)				2	1					
	Scotina celans (Blackwall, 1841)				7						
Lycosidae		193	526	1095	27	57	58	223	481	1343	
	Alopecosa albofasciata (Brullé, 1832)	10						4			
	Alopecosa cuneata (Clerck, 1757)								2		
	Alopecosa farinosa (Herman, 1879)	1						3			
	Alopecosa pulverulenta (Clerck, 1757)	9	113	70		1	3	30	67	13	
	Arctosa figurata (Simon, 1876)	1									
	Arctosa leopardus (Sundevall, 1833)								1		
	Arctosa lutetiana (Simon, 1876)		6								
	Arctosa maculata (Hahn, 1822)					1					
	Arctosa personata (L. Koch, 1872)	8	2					1			
	Aulonia albimana (Walckenaer, 1805)	34	81	41	2	1	1	21	15	19	
	Hogna radiata (Latreille, 1817)	27	8	35	2		8	26	54		
	Pardosa agrestis (Westring, 1861)							12			
	Pardosa alacris (C.L. Koch, 1833)		6			6					only males (see *Pardosa lugubris* gr.)
	Pardosa blanda (C.L. Koch, 1833)			3							
	Pardosa cribrata Simon, 1876							1			
	Pardosa hortensis (Thorell, 1872)	1			1				1		
	Pardosa lugubris gr.		17	25		11	18		4	1	(only females)
	Pardosa palustris (Linnaeus, 1758)			1					3	81	

	Pardosa prativaga (L. Koch, 1870)								1		
	Pardosa proxima (C.L. Koch, 1847)	37		2				54	163	4	
	Pardosa riparia (C.L. Koch, 1833)		126	706					49	1165	
	Pardosa saltans Töpfer-Hofmann, 2000			10			12				only males (see *Pardosa lugubris* gr.)
	Pardosa vittata (Keyserling, 1863)	1						2			
	Piratula hygrophila (Thorell, 1872)			48							
	Piratula latitans (Blackwall, 1841)			85						1	
	Trochosa hispanica Simon, 1870	38	102		9	28		37	68	1	only males (see *Trochosa* sp.)
	Trochosa robusta Simon, 1876	1						6			only males (see *Trochosa* sp.)
	Trochosa ruricola (De Geer, 1778)			1							only males (see *Trochosa* sp.)
	Trochosa sp.	25	60	39	13	4	6	18	44	38	(only females)
	Trochosa terricola Thorell, 1856		5	29		5	10		7	19	only males (see *Trochosa* sp.)
	Xerolycosa miniata (C.L. Koch, 1834)							8	2		
Nemesiidae		7						1			
	Nemesia sp.	7						1			Unknown population (only males). To be compared with *N. transalpina*
Nesticidae								2			
	Eidmannella pallida (Emerton, 1875)							2			
Philodromidae		91			1			28	1	1	

	Philodromus dispar Walckenaer, 1826				1						
	Thanatus arenarius L. Koch, 1872	11						4	1		
	Thanatus atratus Simon, 1875	80						24			
Phrurolithidae		10	34	3		5		14	23	4	
	Phrurolithus festivus (C.L. Koch, 1835)	9	19	3		3		14	12		
	Phrurolithus minimus C.L. Koch, 1839	1	15			2			11	4	
Pisauridae		1	3			2		1			
	Pisaura mirabilis (Clerck, 1757)	1	3			2		1			
Salticidae		18	20	5	20	2		24	2	2	
	Asianellus festivus (C.L. Koch, 1834)	4									
	Chalcoscirtus infimus (Simon, 1868)							2			
	Euophrys frontalis (Walckenaer, 1802)	2	15	3				8		1	
	Evarcha falcata (Clerck, 1757)	1	2								
	Heliophanus cupreus (Walckenaer, 1802)							4			
	Heliophanus flavipes (Hahn, 1832)	3									
	Myrmarachne formicaria (De Geer, 1778)		2								
	Phlegra fasciata (Hahn, 1826)	3		1				5			
	Saitis barbipes (Simon, 1868)				20	2		1			
	Sibianor aurocinctus (Ohlert, 1865)	1	1	1					2	1	
	Talavera aequipes (O. P.-Cambridge, 1871)	4						4			
Tetragnathidae		4	61	47		1	1	9	739	123	
	Pachygnatha degeeri Sundevall, 1830	4	61	47		1	1	9	739	123	

Theridiidae		5	8	17	1	29	1	44	1	6	
	Asagena italica (Knoflach, 1996)							11			
	Enoplognatha thoracica (Hahn, 1833)	1		2		1			1	3	
	Episinus truncatus Latreille, 1809			5	1	2					
	Euryopis episinoides (Walckenaer, 1847)							27			
	Euryopis flavomaculata (C.L. Koch, 1836)		4	3		12				3	
	Neottiura suaveolens (Simon, 1879)	1						1			
	Phylloneta sisyphia (Clerck, 1757)	1									
	Robertus arundineti (O. P.-Cambridge, 1871)	2		3				5			
	Robertus mediterraneus Eskov, 1987		4	4		14	1				
Thomisidae		25	10	26	1	4	3	28	41	40	
	Bassaniodes robustus (Hahn, 1832)	1	1	1				4		1	
	Cozyptila blackwalli (Simon, 1875)	1			1	4					
	Ozyptila atomaria (Panzer, 1801)									1	
	Ozyptila sanctuaria (O. P.-Cambridge, 1871)	20						3	3		
	Ozyptila trux (Blackwall, 1846)			15			3			16	
	Xysticus acerbus Thorell, 1872	1							4		
	Xysticus bifasciatus C.L. Koch, 1837		4	5					20	14	
	Xysticus cristatus (Clerck, 1757)			1					1		
	Xysticus erraticus (Blackwall, 1834)		1	1						2	
	Xysticus gallicus Simon, 1875			2						1	
	Xysticus kochi Thorell, 1872	2	4					21	13	4	
	Xysticus lanio C.L. Koch, 1835			1						1	

Titanoecidae		19						38			
	Nurscia albomaculata (Lucas, 1846)	2						36			
	Titanoeca tristis (L. Koch, 1872)	17						2			
Zodariidae		6	7		2			3	1		
	Zodarion hamatum Wiehle, 1964	6	6		2			2	1		
	Zodarion rubidum Simon, 1914		1					1			
Zoridae		1	2	5	3	3					
	Zora nemoralis (Blackwall, 1861)			4							
	Zora silvestris Kulczynski, 1897	1									
	Zora spinimana (Sundevall, 1833)		2	1	3	3					

Table C.2 Number of traps collected for each habitat type and elevation belt. For each trap, the time of sampling was 14 days. Time span ranged from May to September.

Low-elevation			**Medium-elevation**			**High-elevation**		
Abandoned	**Forest**	**Crop**	**Abandoned**	**Forest**	**Meadow**	**Abandoned**	**Forest**	**Pasture**
111	68	128	83	133	107	72	118	68

Appendix D

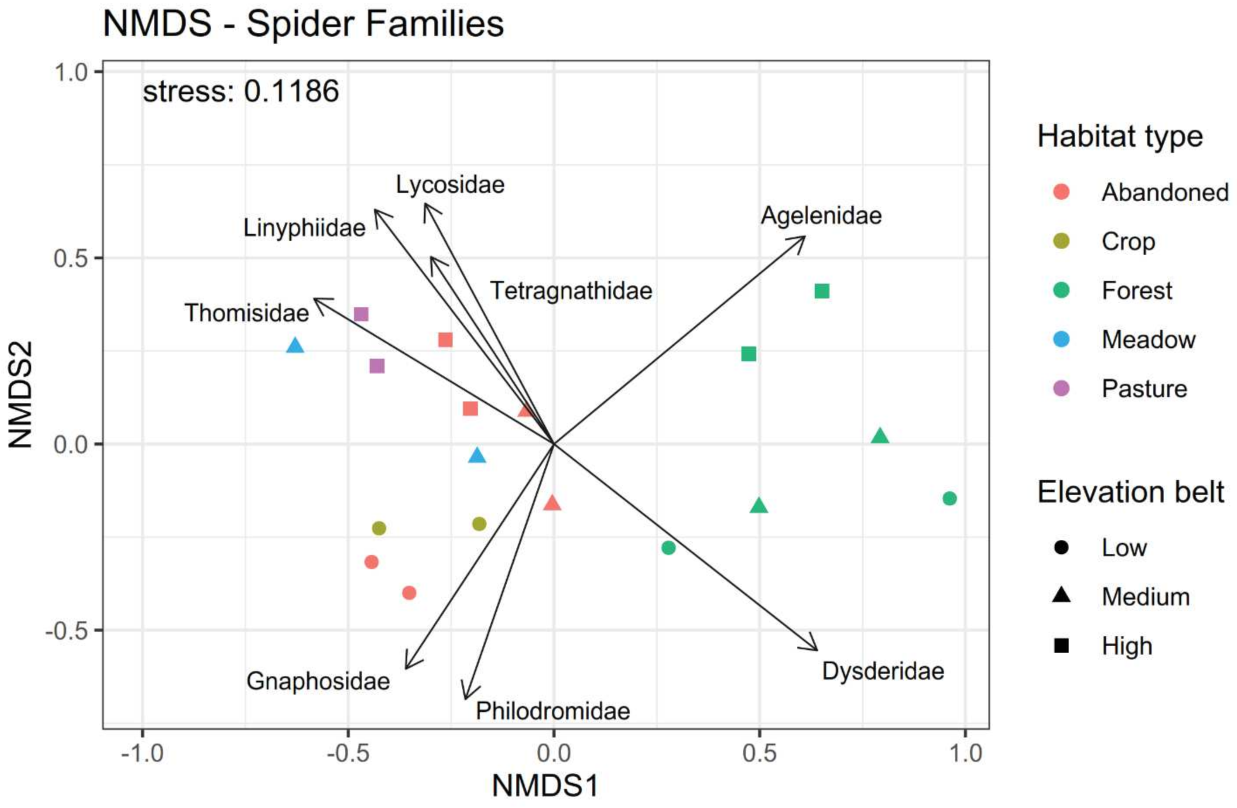


Fig D.1 Non-metric Multidimensional Scaling analysis at the family level. We used only family with at least 100 sampled individuals. Only significant families were plotted: Theridiidae has been included in this analysis, but its vector was not displayed in ordination plot because it was not significant (tested with function *envfit* of package VEGAN).

	Df	Sum of squares	R^2	F	Pr(>F)
Habitat	**4**	**2.644**	**0.61369**	**5.1629**	**0.001*****
Residual	13	1.6644	0.38631		
Total	17	4.3083	1		

Table D.1 Results of PERMANOVA test on community distance at the family level. Bray-Curtis distance has been used.

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