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RESEARCH PAPER

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

Davide Nardi[a,b,c,*], Filippo Giannone[d], Lorenzo Marini[a]

[a]*DAFNAE, University of Padova, Viale dell'Università 16, 35020 Legnaro, Padova, Italy*
[b]*Forest Ecology Unit, Research and Innovation Centre - Fondazione Edmund Mach via E. Mach, 1-San Michele all'Adige 38010 TN, Italy*
[c]*Institute for Sustainable Plant Protection - National Research Council (IPSP-CNR), via Madonna del Piano 10, 50019, Sesto Fiorentino, Florence, Italy*
[d]*via J. della Quercia 13E, Padova, Italy*

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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: 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., 2017). In the last decades, European conifer forests have experienced several extreme events

*Corresponding author at: DAFNAE, University of Padova: Universita degli Studi di Padova, Via dell'Università 16, 35020 Legnaro, PD, Italy.
E-mail address: davide.nardi.1@phd.unipd.it (D. Nardi).

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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 (Bouget & Duelli, 2004; Buddle et al., 2000; Thorn 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 (Elek et al., 2018; Kašák et al., 2017; Phillips et al., 2006; Wermelinger et al., 2017). 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 & 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 & Cardoso, 2014; Pedley & 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

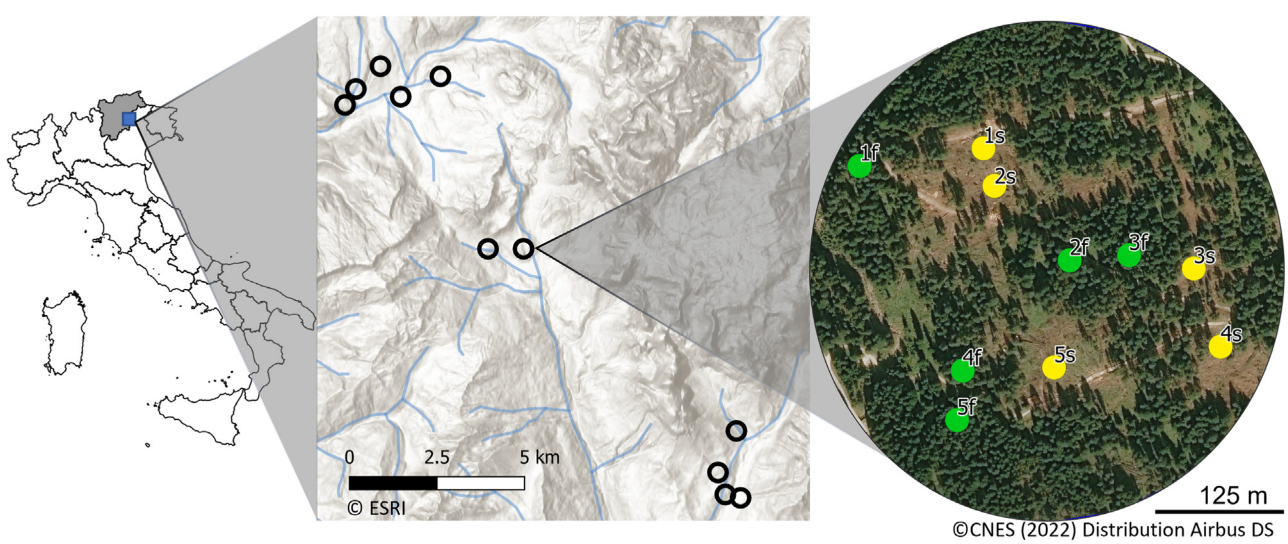

Fig. 1. Sampling design. Sampling was carried out in Trentino (Italy) within the natural park “Parco Paneveggio - Pale di San Martino”. Eleven landscapes (black circles) were chosen in wind-damaged areas to obtain statically orthogonal gradients in elevation, slope, and aspect. Within each habitat type, 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).

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).

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 5-10 cm height) to reduce small vertebrate mortality. 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 collection, arthropods were stored in ethanol for 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 followed 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 and no-significant interactions ($P>0.05$) were excluded in the final models using a backward deletion procedure. 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 & 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 & 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 & Weisberg, 2019), LME4 (Bates et al., 2015) packages. DHARMa (Harting, 2021) package was used for residuals diagnostic.

Dispersal trait analysis

Finally, we tested 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 macropterous species, in which wings are present in at least one sex and brachypterous species, in which wings are not present. For each species, wing morphology was retrieved from the literature (Brandmayr et al., 2005; Casale et al., 1982; Freude et al., 2004) and coded as binary variable (value 1: macropterous species; value 0: brachypterous species). 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, Tables C.1, C.2, C.3). 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 type x elevation, P = 0.04) (Fig. 2A). We found no significant effect of slope on ground beetle density. Spiders showed an opposite pattern (Fig. 2B): in windfalls abundance increased with elevation while in forests we observed a negative effect of elevation

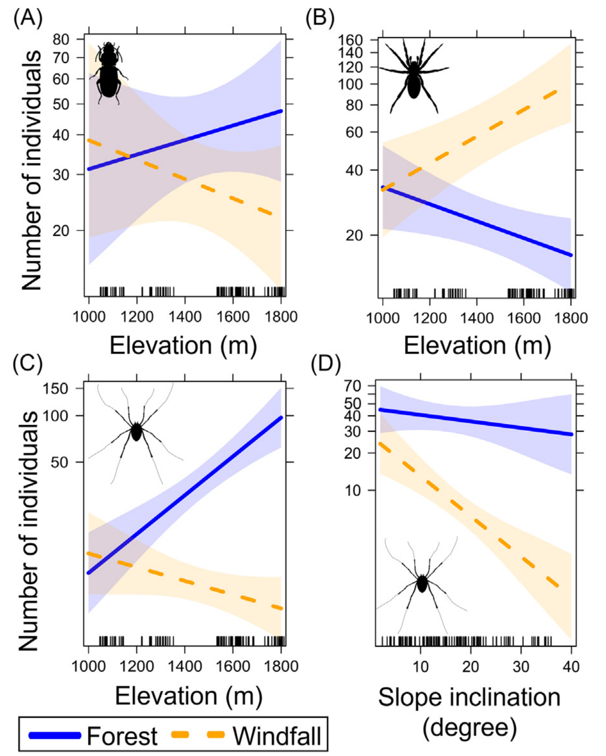

Fig. 2. Interactive effect of topography and habitat type on activity density. Activity density of ground beetles (Fig. 2A), spiders (Fig. 2B) and harvestmen (Fig. 2C-D) varied along elevation and slope. Only significant interactions between elevation/slope and habitat type (i.e. forest and windfall) 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.

(habitat type x elevation: $P < 0.001$). The activity density of harvestmen increased in forests and decreased in windfalls along the elevation gradient (habitat type x elevation, $P < 0.001$). Overall, lower activity density was observed in windfalls (habitat type, $P < 0.001$) (Fig. 2C). In windfalls, activity density of harvestmen decreased with increasing slope (slope x habitat type: P = 0.002) (Fig. 2D).

For species richness, we did not find any difference between habitat types for ground beetles (Fig 3A). For spiders, species richness was higher in windfalls than in forest (habitat type, $P < 0.001$), while an opposite trend was observed for harvestmen (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.

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

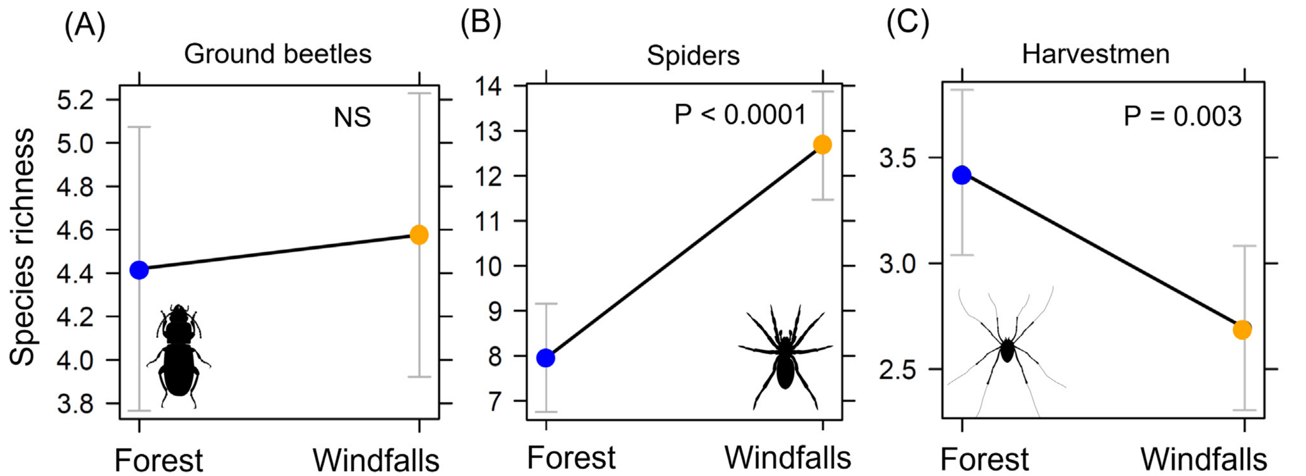

Fig. 3. Species richness in forests and windfalls. Species richness of ground beetles (Fig. 3A), spiders (Fig. 3B) and harvestmen (Fig. 3C) in two habitat types (forest and windfalls). Ground beetles showed no effect of wind disturbance, while spider species richness increased in windfalls and harvestmen 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.

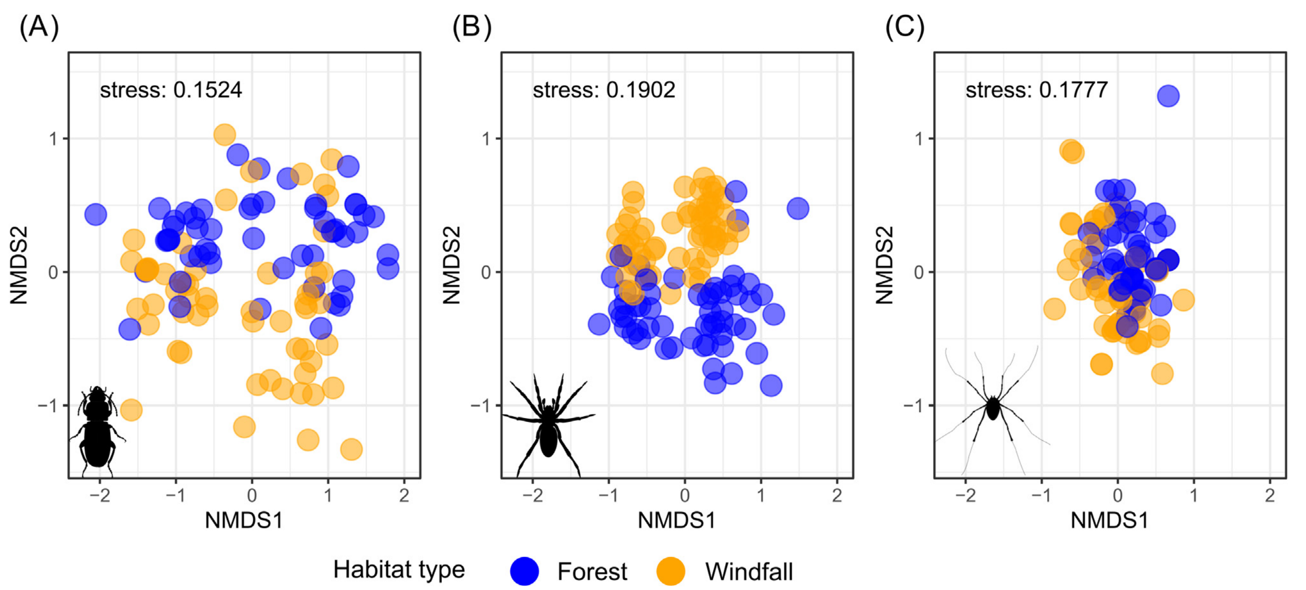

Fig. 4. NDMS ordination plots of forest and windfall communities. For ground beetles (Fig. 4(A), spiders (Fig. 4B) and harvestmen (Fig. 4C) NMDS ordinations of communities belonging to intact forest (blue dots) and windfalls (orange dots) were computed based on the Chao dissimilarity index (abundance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

(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: $P = 0.001$, $R^2 = 0.13$).

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).

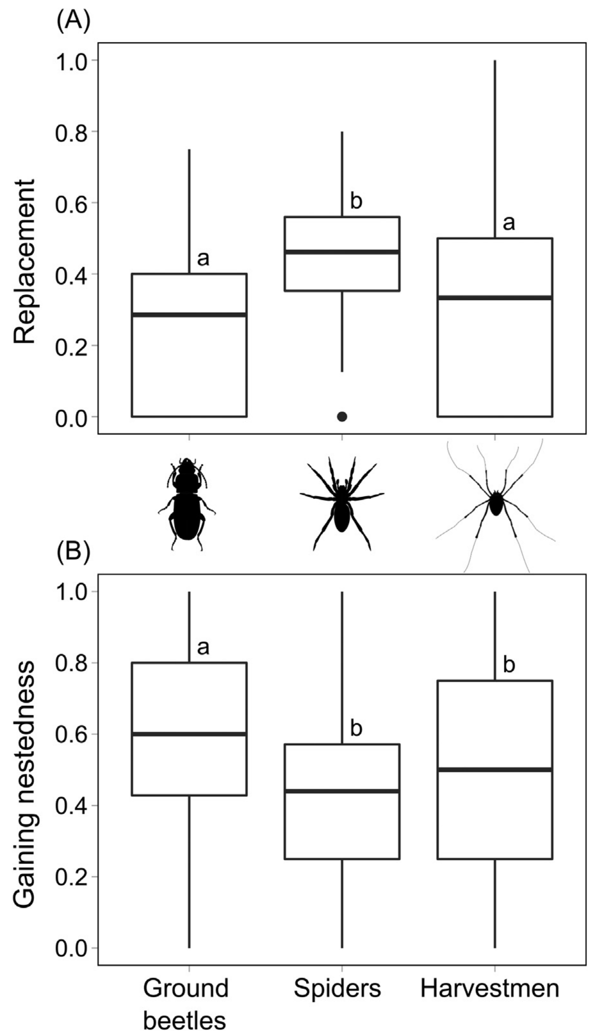

Fig. 5. Components of beta diversity between forest and windfall. For each taxon, we showed neutral replacement (Fig. 5A) and gaining nestedness (Fig. 5B) between neighboring forest-windfall communities. Letters indicate significant differences in the post-hoc test, and refer to linear mixed-effect models. 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). In particular, windfall communities hosted more species with long dispersal strategies, i.e. high ballooning propensity for spiders and macropterous species for ground beetles (P value for ground beetles = 0.008; P value for spiders = 0.0001).

Discussion

Our observational study quantified the short-term response to wind disturbance of ground-dwelling

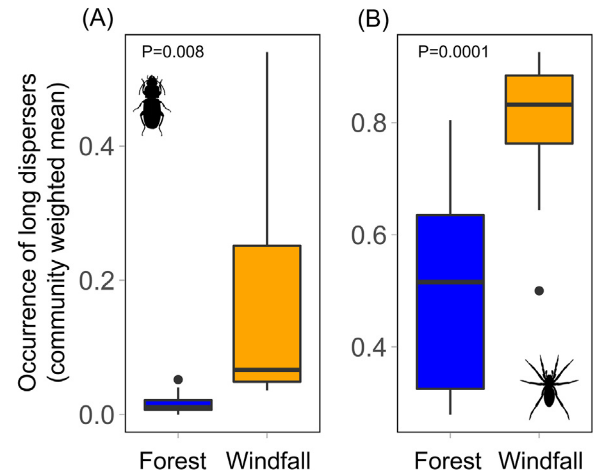

Fig. 6. Community weighted means of dispersal strategies in forest and windfall habitats. For ground beetles (Fig. 6A) and spiders (Fig. 6B), we computed community weighted mean of dispersal strategies (binary variable: 1 for long dispersers, 0 for short dispersers). The response variable varies between 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.

communities in temperate forest ecosystems. Although several studies investigated the effect of forest disturbance (e.g. 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 compounded 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 & 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 (De Smedt et al., 2019; Kataja-aho et al., 2016; 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 & 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 arthropod communities. 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 (Malumbres-Olarte et al., 2013; Schaffers et al., 2008). 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 & 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.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2022.11.004.

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