



Effects of post-mining forest restoration and alternative land uses on ground-dwelling arthropods in Ghana

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Abstract

In an Afrotropical region experiencing massive deforestation, restoration approaches should provide sustainable solutions for recovering biodiversity. Arthropods are a sensitive taxonomic group for habitat alteration by deforestation and can be good indicators for restoration studies. Ground-dwelling arthropods provide important ecosystem functions, such as predation or organic matter decomposition, thereby contributing to ecosystem functionality. The consequences of post-mining management on arthropods in the Afrotropical region remain understudied. We carried out a comprehensive sampling of ground-dwelling arthropods in the dry and wet seasons across four land-use types in the semi-deciduous forest zone of Ghana. We then analysed whether the specific tree communities, vegetation structure and seasonal differences affected arthropod communities in the restored post-mining forest compared to the dominant alternative land-use type (agroforestry plantation), a natural reference (natural forest) or an unmanaged former mining area (gravel mine). In total, 43,364 arthropods were sampled and assigned to 78 taxonomic groups representing 14 order/sub-order, 28 beetle families, 25 spider families, 5 hunting guilds of spiders and 6 trophic groups of beetles. Overall, Araneae, Coleoptera, Hymenoptera and Orthoptera all had higher activity densities in the wet season. The vegetation structure of the three land-use types with trees supported a greater overall activity density of arthropods and a more diverse functional composition compared to the unmanaged gravel site. Pronounced variation between the dry and wet seasons further influenced the taxonomic and functional composition. The active forest restoration of this post-mining area is a promising approach to drive arthropod communities towards a comparable state observed in the natural forest.

Keywords Afrotropical · Arthropod community · Functional composition · Post-mining · Vegetation complexity

Introduction

Arthropods play a key role in ecosystem functioning and provide important ecosystem services for human societies, including local communities in Western Africa (Culliney, 2013; Høye & Culler, 2018; Isaacs et al., 2009; Sagi & Hawlena, 2021). Between 5 and 10 million terrestrial arthropod species have been described worldwide (Novotny et al., 2002; Ødegaard, 2000; Stork, 2018), of which up to 3.7 million species are found in the tropics (May, 2010). The Afrotropical region features a wide range of natural habitats with diverse plant and animal communities (Stuart et al., 1990), many of which are endemic to the region. In

terms of ecosystem services provided by arthropods (Biondi et al., 2015; Dangles & Casas, 2019), pollination, nutrient regulation, soil formation and pest control contribute to human well-being (Birkhofer et al., 2018; Rader et al., 2016; Schowalter, 2017). Thereby, arthropods contribute to global food security (van der Sluijs & Vaage, 2016) and consequently reduce poverty (Dangles & Casas, 2019), as for example, predators (e.g. spiders) prey on herbivorous organisms, which could become pests on crops (Nyffeler et al., 2016).

Arthropod populations and diversity are threatened by human activities stemming from agricultural intensification, mining and land-use conversion or habitat loss (Birkhofer et al., 2015; Dampthey et al., 2022a; Picanço et al., 2017; Seibold et al., 2019). Mining has been a crucial economic sector in many developing countries but comes with costs for biodiversity and interrupts the provision of several ecosystem services to human society (Asare et al., 2022; Ofosu

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et al., 2020; Schueler et al., 2011; Sonter et al., 2018). For instance, surface mining leads to the degradation of forests that would have otherwise provided habitat for pollinating or seed-dispersing arthropods, with consequences for local and global food security (Sonter et al., 2018). In addition, a shortage of productive land coupled with changing local and regional weather conditions because of land degradation and climate change leads to a decline in farm productivity and an increase in food insecurity globally (Ime & Ekong, 2015). Similarly, the removal of trees during mining eliminates the ability of forests to store carbon, with severe implications for climate change (Ontl et al., 2020). Moreover, a land-use change that involves the conversion of a particular land-use type (e.g. natural forest) to alternative land use (e.g. agroforestry plantations) is known to result in a loss of arthropod biodiversity in some regions (e.g. Newbold, 2018). The high rate of conversion of tropical forests to other land uses is also anticipated to have consequences for both local and regional biodiversity, with cascading effects on other ecological processes (Schroeder et al., 2021). For instance, it is very obvious that the conversion of forests to agricultural lands or recreational parks affects arthropod diversity on a global scale (Millard et al., 2021; Perry et al., 2016), but the effect of restoring post-mining areas through restoration or agroforestry on arthropods is relatively unknown in Ghana and responses may differ among different taxonomic or functional arthropod groups. Restoration in Ghana sometimes takes the form of agroforestry, where economic and ecological valued tree species are interplanted with food crops to meet societal needs or the form of enrichment planting to restore degraded forests (Dampsey et al., 2021). Although several studies have discussed the devastating effects of land-use change on arthropods elsewhere in the world (e.g. Cardoso et al., 2020; Gagnarli et al., 2021), the consequences of land-use conversion and post-mining restoration in Ghana and Western Africa, in general, remain understudied.

In addition to the impact of land-use changes, pronounced seasonal differences will also affect the taxonomic and functional composition of arthropod communities (Wardhaugh et al., 2018). In Ghana, the two major seasons are based on the amount of precipitation, differences in temperature and the number of dry months (Owusu & Waylen, 2012). The characteristic rainfall in the wet season (April to July) should facilitate the emergence of arthropods from soil and the development of large patches of potential host plants (Basset et al., 2015). However, the dry season, with its long period of drought conditions, is accompanied by water stress-inducing physiological constraints and limited resource availability, thereby limiting the ability of arthropods to perform essential ecological functions and other services (Huberty & Denno, 2004).

To address the question of how post-mining restoration affects arthropod communities compared to a natural reference system, an alternative land-use type and an unmanaged former mining area in the two major seasons in Ghana, we tested the following hypotheses: (i) land-use types with diverse tree communities and heterogeneous vegetation structure (natural and restored forest) support a higher number of arthropod orders, functional groups and overall activity density than in agroforestry plantation and former mining area and (ii) the effect of land-use types on the taxonomic and functional composition of arthropods depends on the season with the strongest expected differences between land-use types with trees and agroforestry plantation and former mining area in the wet season.

Materials and methods

Study area

The studied land-use types include the following: (1) an actively “restored forest” as restoration activity (Terchire restoration area; RF), (2) an “agroforestry plantation” as an alternative land-use (Bosomkese forest reserve; AF), (3) a “natural forest” as a natural reference (Asukese forest reserve; NF) and (4) an unmanaged “gravel site” as an unmanaged system (Terchire abandoned gravel mine site; GS). All land-use types lie in a semi-deciduous forest zone (SDFZ) and are located in the Ahafo and Bono regions of Ghana (Fig. 1; Dampsey et al., 2022b). The forest zone is characterised by a mean daily temperature of 20 °C and annual precipitation ranging between 900 and 1500 mm (rainfall peaks between July and August; Dampsey et al., 2021).

The RF is located in Terchire (7° 14' 4.78" N, 2° 10' 49.88" W), about 24 km from Sunyani, the Bono regional capital of Ghana. It was actively restored after gravel mining by planting leguminous cover crops (e.g. *Mucuna bracteata*, *Luffa egyptiaca*, *Pueraria phaseoloides*) and trees, both indigenous (e.g. *Morinda lucida* Benth, *Terminalia suberba* Engl. & Diels, *Albizia zygia* (DC) J. F. Machr, *Mangifera indica* L., *Ceiba pentandra* (L.) Gaertn.) and exotic (e.g. *Tectona grandis* L. f., *Cedrella odorata* L., *Senna siam* (Lam.) H. S. Irwin & Barneby) species after soil improvement and cover crops to provide essential ecosystem goods and services to local communities (Dampsey et al., 2022b). The vertical profile of tree communities in RF is mainly uniform and characterised by upper canopy trees. The AF (7° 6' 20.76" N, 2° 15' 22.64" W) is a degraded forest that has been subjected to agroforestry programmes (food crops interplanted with trees) to supply both food and energy needs as well as environmental benefits to local communities. It is characterised by frequent annual wildfire events (Dampsey

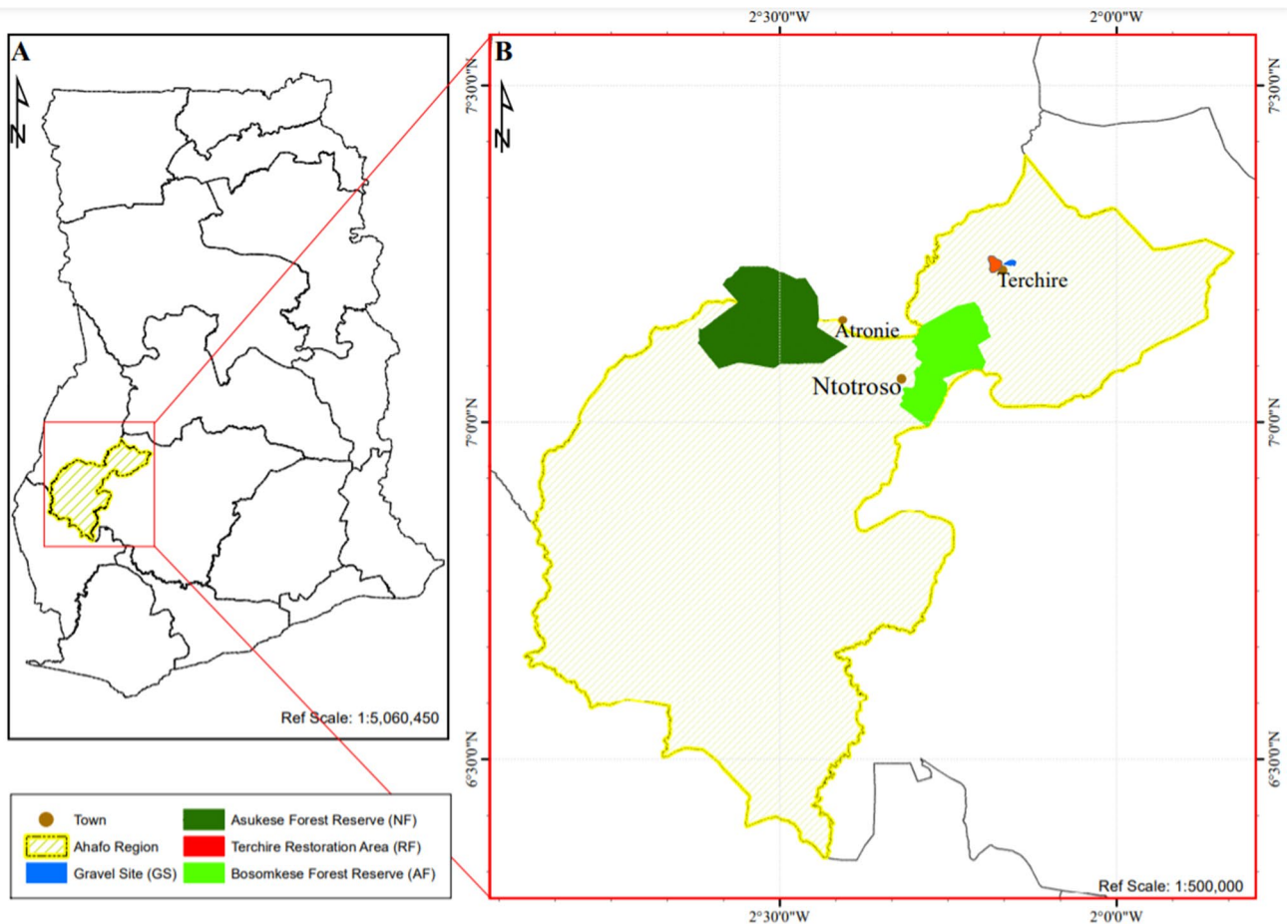


Fig. 1 Map of Ghana (A) with the study region in Ghana and the studied land-use types (B)

et al., 2020). The NF ($7^{\circ} 9' 13.72''$ N, $2^{\circ} 31' 4.96''$ W) is a protected forest reserve under strict restrictions against anthropogenic activities. It is composed of native tree species, including *Celtis mildbraedii*, *Triplochiton scleroxylon*, *Cola gigantean*, *Nesogordonia papaverifera*. The vertical profile of tree communities in NF is a multi-layered structured with shrub layer, lower canopy, upper canopy and emerging trees. The GS is a four-hectare abandoned gravel mine ($7^{\circ} 14' 9.26''$ N, $2^{\circ} 9' 36.13''$ W) located about 1.8 km from RF and colonised by the following invasive species: *Chromolaena odorata* and *Pennisetum purpureum* (Dampney et al., 2020). Table 1 provides an overview of selected vegetation attributes in all land-use types (Dampney et al., 2020, 2021).

Sampling design

The four land-use types were studied across both seasons (dry and wet) in the semi-deciduous forest zone (SDFZ) of Ghana. Each land use was studied in eight replicate 20×20 m plots, resulting in 32 study plots. Basic

vegetation attributes (Table 1) were surveyed and used to describe the major dendrological characteristics of each land-use type (see also Dampney et al., 2020, 2021). A standardised trapping method involving the use of pitfall traps was used to sample and estimate the activity density (A_D: number of samples caught divided by the sampling effort) of ground-dwelling arthropods based on their locomotory activities (Greenslade, 1964; Perner & Schueler, 2004).

Ground-dwelling arthropod communities were continuously sampled, with five pitfall traps in each plot being emptied weekly for 10 weeks in each sampling season. The first campaign was conducted in the dry season (January to March 2019), followed by the wet season campaign (June to August 2019). Pitfall traps were filled with a 50:50% mixture of propylene glycol and water, and all pitfall traps were covered by small roofs to avoid dilution of the trap liquid by rain (Underwood & Quinn, 2010). Pitfall trap samples were stored in 70% ethanol and later sorted into taxonomic groups (order, suborder or family) according to available identification keys (for spiders; Dippenaar-Schoeman & Jocqué,

Table 1 Vegetation structure (means and standard errors) of tree communities in the studied land-use types

| Vegetation attributes | Land uses | | |
|--------------------------------------|---|--|---|
| | Restored forest | Agroforestry plantation | Natural forest |
| Tree species (n/ha) | 9 ± 1.7 | 7 ± 0.9 | 12 ± 0.9 |
| Tree abundance (n/ha) | 30 ± 3.6 | 27 ± 2.9 | 23 ± 2.7 |
| Tree diameter (cm) | 30.5 ± 4.7 | 38.5 ± 3.8 | 51.4 ± 5.4 |
| Basal area (m ² /ha) | 3.0 ± 0.9 | 4.7 ± 0.4 | 6.9 ± 1.2 |
| Tree height (m) | 13.3 ± 0.3 | 15.2 ± 0.8 | 14.3 ± 0.2 |
| Deadwood volume (m ³ /ha) | 1740.2 ± 338 | 5816.7 ± 1209.0 | 7626.1 ± 2277.2 |
| Litter depth (cm) | 2.8 ± 0.1 | 2.1 ± 0.1 | 3.1 ± 0.1 |
| Canopy openness (%) | 19.2 ± 1.4 | 20.2 ± 0.9 | 12.7 ± 0.7 |
| Species composition | 18% exotic, 82% native | 6% exotic, 94% native | 100% native |
| Dominant tree species | <i>leucaena leucocephala</i> , <i>Senna siamea</i> , <i>Mangifera indica</i> , <i>Morinda lucida</i> , <i>Terminalia superba</i> , <i>Ammonia muricata</i> , <i>Albizia zygia</i> , <i>Blighia sapida</i> | <i>Ceiba pentandra</i> , <i>Triplochiton scleroxylon</i> , <i>Cedrela odorata</i> , <i>Terminalia superba</i> , <i>Cola gigantea</i> , <i>Mangifera indica</i> , <i>Dialium guineense</i> , <i>Microdesmis puberula</i> , <i>Cola nitida</i> , <i>Celtis mildbraedii</i> , <i>Albizia zygia</i> , <i>Alstonia boonei</i> | <i>Celtis mildbraedii</i> , <i>Triplochiton scleroxylon</i> , <i>Cola gigantea</i> , <i>Nesogordonia papaverifera</i> , <i>Celtis aldolfi-frider</i> , <i>Albizia zygia</i> , <i>Chrysophyllum albidum</i> , <i>Cola nitida</i> , <i>Tetrapleura tetraptera</i> , <i>Sterculia rhinopetala</i> , <i>Entandrophragma utile</i> |
| | | | Gravel site |
| | | | 1 ± 0.3 |
| | | | 2 ± 0.4 |
| | | | 9.2 ± 3.5 |
| | | | 0.9 ± 0.3 |
| | | | 4.4 ± 1.7 |
| | | | 0.0 ± 0.0 |
| | | | 0.0 ± 0.0 |
| | | | 91.4 ± 0.9 |
| | | | – |
| | | | <i>Anacardium occidentale</i> |

Fig. 2 Non-metric multidimensional scaling ordination based on log-transformed ($\log(x+1)$) activity densities of arthropod orders or suborders and Bray–Curtis similarities between plots of different land-use types (○ Restored forest, × Agroforestry plantation, + Natural forest and ◇ Gravel site) and seasons (green = wet, red = dry). The 2-d stress value is 0.06. Symbols of each land-use type and season combination are connected by minimum spanning trees

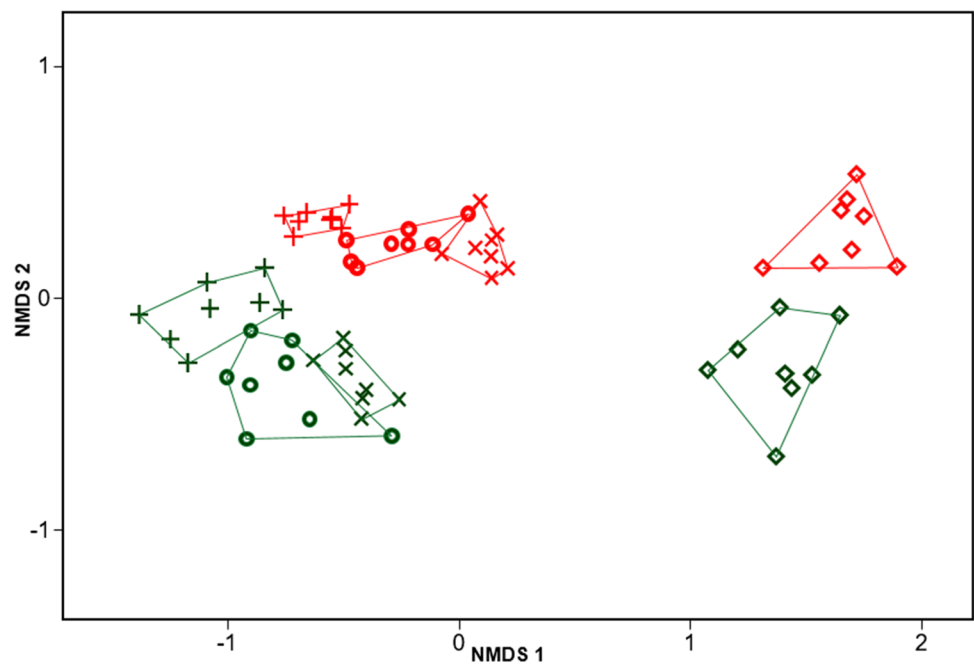
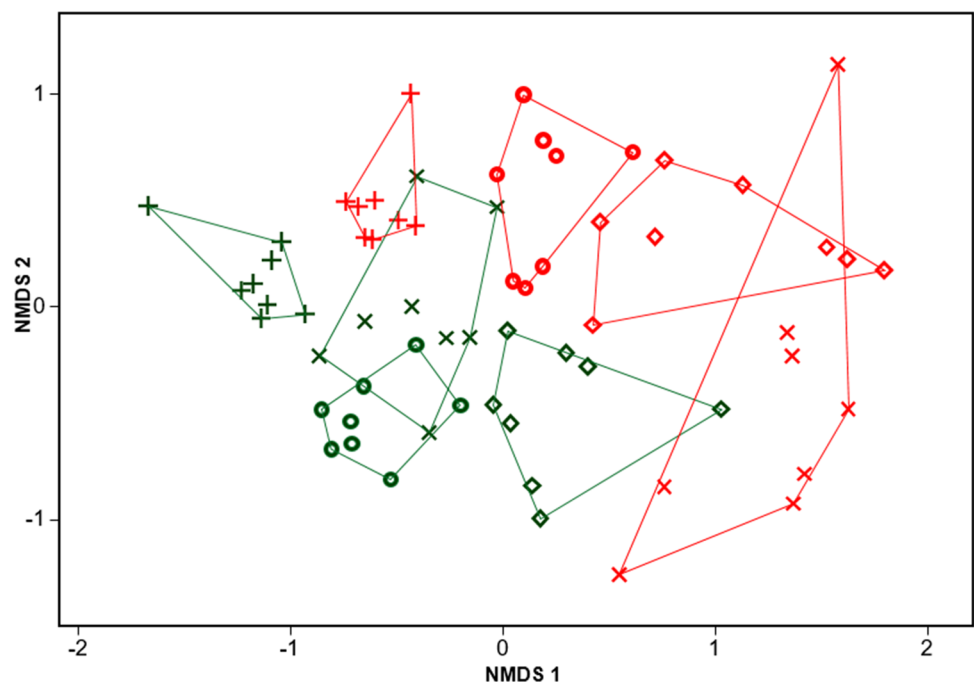


Fig. 3 Non-metric multidimensional scaling ordination based on log-transformed ($\log(x+1)$) activity densities of spiders and Bray–Curtis similarities between plots of different land-use types (○ Restored forest, × Agroforestry plantation, + Natural forest and ◇ Gravel site) and seasons (green = wet, red = dry). The 2-d stress value is 0.19. Symbols of each land-use type and season combination are connected by minimum spanning trees



1997) and insects; Picker (2012). Individuals of the orders Coleoptera and Araneae were always sorted at the family level. The Coleoptera (beetle) families were subsequently classified into trophic groups (detritivores, herbivores, carnivores and fungivores; some families cannot be assigned to one of those categories leading to the combined classes herbivores & detritivores and carnivores & detritivores; Lassau et al., 2005). The Araneae (spider) families were also classified into hunting guilds (sensing web, ground hunters,

ambush hunters, other hunters and specialist spiders; Cardoso et al., 2011).

Data analyses

Arthropod community data for plots within each land-use type were pooled together and log-transformed [$\log(x+1)$]. Activity density (A_D) of arthropods for land-use types and

Table 2 Contribution of spider families to the dissimilarities in community composition between the wet and dry season plots based on similarity percentage analysis (SIMPER)

| Family | Wet AD | Dry AD | Diss | Diss./SD | Contrib.% | Cum.% |
|-----------------|--------|--------|------|----------|-----------|-------|
| Salticidae | 1.83 | 1.52 | 6.89 | 1.49 | 15.83 | 15.83 |
| Zodariidae | 2.46 | 1.22 | 6.75 | 1.59 | 15.50 | 31.32 |
| Ctenidae | 1.60 | 0.76 | 5.66 | 1.47 | 12.99 | 44.31 |
| Corinnidae | 1.35 | 0.63 | 5.06 | 1.26 | 11.62 | 55.93 |
| Lycosidae | 2.83 | 2.70 | 4.30 | 1.43 | 9.88 | 65.81 |
| Cyrtoucheniidae | 0.85 | 0.14 | 3.98 | 1.13 | 9.15 | 74.96 |

AD, average activity density; Diss., average dissimilarity; SD, standard deviation; Contrib.%, contribution percentage to overall dissimilarity; Cum.%, cumulative contribution percentage

seasons was estimated based on the number of individuals sampled divided by the sampling effort (Greenslade, 1964).

A non-metric multidimensional scaling ordination (NMDS) based on Bray–Curtis similarities was created to visually represent the multivariate relationship within and between sampling plots of different land-use types and seasons. The goodness of fit of NMDS ordinations was evaluated using the 2-d stress value (Clarke et al., 2014). For the NMDS based on the taxonomic composition of all arthropods, vectors were superimposed for orders with Pearson correlation coefficients > 0.2 with axis scores. For the identification of Coleoptera and Araneae families and functional groups that were characteristic of land-use types or seasons, similarity percentage analysis (SIMPER) was used based on Bray–Curtis similarity and a cut-off value of 70% for the total contribution (Sommerfeld & Clarke, 2013). Statistical analyses and visualisations were carried out with the Plymouth Routines in Multivariate Ecological Research (PRIMER vs 7; Clarke & Gorley, 2015) or R statistical computing software version 2.15.3 (R Core Team, 2019).

Results

Arthropod taxonomic composition

In total, 43,364 arthropods were sampled and assigned to 78 taxonomic groups representing 14 order/sub-order (“Appendix 1”), 28 beetle families (divided into 6 trophic groups) and 25 spider families (divided into 5 hunting guilds). The arthropod communities at the former gravel mine are unique for both seasons, followed by a gradient from the agroforestry plantation to the restored and the natural forest communities with increasing activity densities of Blattodea, Julida, Hymenoptera, Coleoptera and Araneae along that gradient independent of the season (Fig. 2). The restored forest plots have an intermediate position between the agroforestry plantation and the natural forest arthropod communities. Within land-use types, Hemiptera had a higher activity density in the dry season compared to the wet season. Blattodea and Julida had the highest activity density in the natural forest

and were absent from the gravel site. Within land-use types, Orthoptera had a higher activity density in the wet season, and Polydesmida were only present in the wet season.

Spider family composition

The total activity density of spiders was higher in NF (3.03) than RF (2.79), AF (1.59) and GS (1.35) and also higher in the wet (5.44) than in the dry season (3.32). The families Lycosidae, Salticidae and Zodariidae, dominated communities, amounting to more than 50% of all individuals in each of the four land-use types. Most families (e.g. Corinnidae, Ctenidae, Migidae, Zodariidae) had higher activity densities in the wet season, except Oxyopidae, which had a higher activity density in the dry season, and Lycosidae and Salticidae, which did not differ much between seasons (Fig. 3). Spider family composition showed a gradient from the dry season agroforestry plantation and the gravel site for both seasons towards the restored forest and the natural forest plots for both seasons. For spider communities, the wet season agroforestry plots hold an intermediate position between the restored and natural forest plots.

The average dissimilarity between the dry and wet season plots was 44% and was driven by a higher activity density of Salticidae, Zodariidae, Ctenidae, Corinnidae, Lycosidae and Cyrtoucheniidae in the wet season (Table 2). In terms of dominance, the dry season plots were dominated by Lycosidae (28% of all individuals), Zodariidae (25%), Salticidae (15%) and Corinnidae (12%) and differed from wet season plots due to an even higher dominance of Lycosidae (52%) but lower dominance of Zodariidae (16%) and Salticidae (12%) in the wet season.

Spider hunting guilds

Ground hunters ($A_D = 4.13$) were the most dominant group across land-use types, followed by other hunters ($A_D = 2.61$), specialists ($A_D = 1.59$), sensing web ($A_D = 0.35$) and ambush hunters ($A_D = 0.07$). Ground hunters were more active in RF than GS, AF and NF (Fig. 4A). Sensing spiders were rather active in the AF than

Fig. 4 Box plots for activity densities in different hunting guilds (**A**, ground hunters; **B**, sensing web; **C**, other hunters; and **D**, specialist spiders) between land-use types: RF, restored forest; AF, agroforestry plantation; NF, natural forest; GS, gravel site. Single points indicate outliers based on median and interquartile deviation method (IQD)

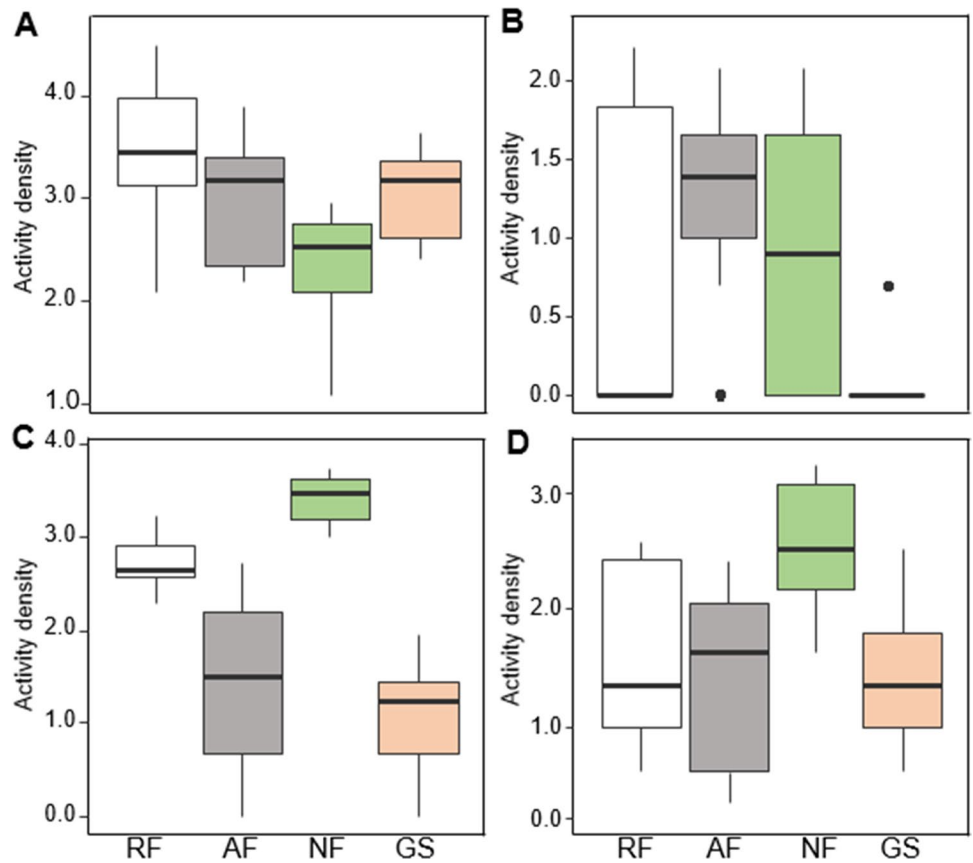
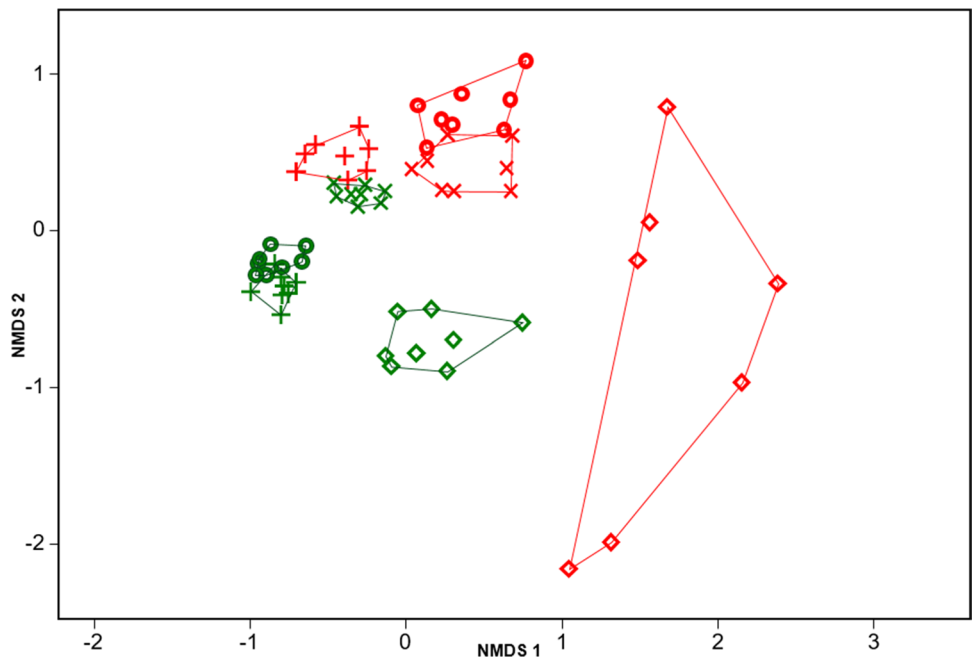


Fig. 5 Non-metric multidimensional scaling ordination based on log-transformed ($\log(x+1)$) activity densities of beetles and Bray–Curtis similarities between plots of different land-use types (○ Restored forest, × Agroforestry plantation, + Natural forest and ◇ Gravel site) and seasons (green = wet, red = dry). The 2-d stress value is 0.13. Symbols of each land-use type and season combination are connected by minimum spanning trees



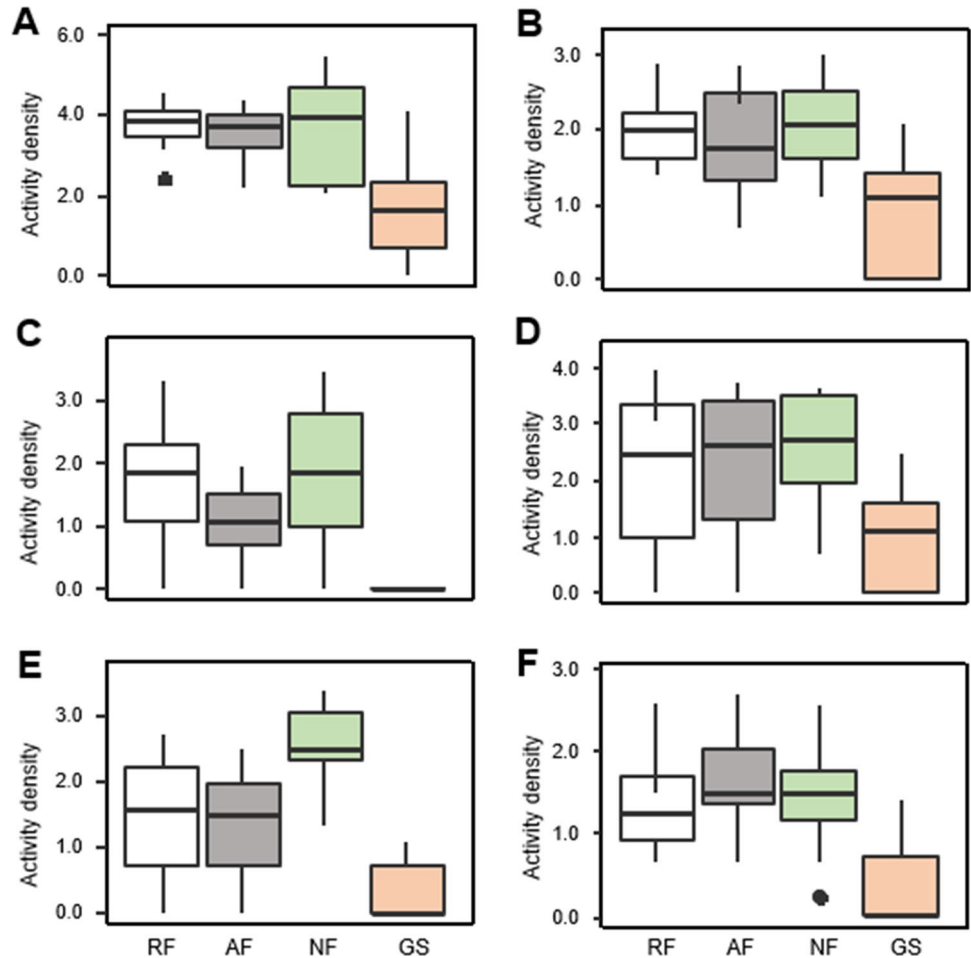
NF, RF and GS (Fig. 4B). Other hunters were also more active in NF than RF, AF and GS (Fig. 4C). For specialist's

spiders, higher activity density was recorded for NF compared to RF, GS and AF (Fig. 4D).

Table 3 Contribution of beetle families to the dissimilarities in community composition between the wet and dry season plots based on similarity percentage analysis

| Family | Wet AD | Dry AD | Diss | Diss./SD | Contrib. % | Cum. % |
|---------------|--------|--------|------|----------|------------|--------|
| Scarabaeidae | 3.47 | 0.94 | 9.86 | 1.58 | 15.06 | 15.06 |
| Carabidae | 2.95 | 0.97 | 7.69 | 1.59 | 11.76 | 26.82 |
| Tenebrionidae | 1.08 | 2.24 | 5.90 | 1.34 | 9.02 | 35.84 |
| Staphylinidae | 2.00 | 1.00 | 5.49 | 1.50 | 8.38 | 44.22 |
| Hydrophilidae | 1.66 | 0.19 | 5.11 | 0.91 | 7.81 | 52.03 |
| Histeridae | 1.46 | 0.10 | 4.69 | 1.09 | 7.17 | 59.20 |
| Cetoniidae | 1.07 | 0.09 | 4.33 | 1.04 | 6.62 | 65.82 |
| Nitidulidae | 1.52 | 1.57 | 4.04 | 1.15 | 6.17 | 71.99 |

Fig. 6 Box plots for activity densities in different trophic groups of beetle functional groups (A, detritivores; B, herbivores; C, fungivores; D, carnivores; E, carnivores & detritivores and F, herbivores & detritivores) between land-use types: RF, restored forest; AF, agroforestry plantation; NF, natural forest and GS, gravel site. Single points indicate outliers based on median and interquartile deviation method (IQD)



Beetle family composition

The taxonomic composition of beetle communities differed significantly between land-use types ($F_{3,27} = 14.52$; $p < 0.001$) and seasons ($F_{1,27} = 46.14$; $p < 0.001$). The differences between land-use types did depend on the season ($F_{3,27} = 10.80$; $p < 0.001$). Pairwise statistical comparisons indicated significant differences in family composition between beetle communities of the natural forest and the agroforestry plantation ($t = 4.41$, $p < 0.001$), restored forest

($t = 3.24$, $p < 0.001$), gravel site ($t = 4.50$, $p < 0.001$) and between the restored forest and the agroforestry plantation ($t = 2.02$, $p = 0.005$), gravel site ($t = 3.86$, $p < 0.001$) as well as between the agroforestry plantation and the gravel site ($t = 3.78$, $p < 0.001$). Beetle communities at the former gravel mine were unique and more heterogeneous during the dry season than during the wet season, with a higher activity density of Elateridae at the gravel site plots (Fig. 5). The beetle communities in the wet season restored and natural forest plots resembled each other and were characterised

by higher activity densities of Histeridae, Hydrophilidae and Staphylinidae. While beetle communities did not differ between the natural and restored forests in the wet season, they differed in the dry season. Beetle communities in the agroforestry plantation in the wet season resembled forest communities in the dry season more than other communities in habitats with trees in the wet season.

In terms of dominance, the dry season plots were dominated by Tenebrionidae (36% of all individuals), Nitidulidae (20%), Carabidae (10%) and Erotylidae (8%) and differed from wet season plots by and even higher dominance by Scarabaeidae (26%) and Carabidae (22%) but lower dominance of Staphylinidae (13%), Nitidulidae (9%) and Cetoniidae (7%). The average dissimilarity between the dry and wet season plots was 65% and was driven by a higher activity density of Scarabaeidae, Carabidae, Staphylinidae, Hydrophilidae, Histeridae and Cetoniidae in the wet season but a higher activity density of Tenebrionidae and Nitidulidae in the dry season (Table 3).

Beetle trophic groups

Based on the activity density of beetle trophic groups, the following order reflects their dominance across land-use types: detritivores (67%), carnivores (18%), herbivores (8%) and fungivores (7%). The activity density of detritivores ($F_{3,28} = 29.95$; $p < 0.001$), carnivores ($F_{3,28} = 13.76$; $p < 0.001$), herbivores ($F_{3,28} = 31.64$; $p < 0.001$), fungivores ($F_{3,28} = 46.14$; $p < 0.001$), herbivores & detritivores ($F_{3,28} = 33.34$; $p < 0.001$) and carnivores & detritivores ($F_{3,28} = 46.64$; $p < 0.001$) differed significantly between land-use types. Except for beetle families classified as herbivores and detritivores combination (Fig. 6F), the natural forest had significantly higher activity densities for all trophic groups. The gravel site recorded the lowest activity density for all trophic groups (Fig. 6).

Discussion

Our comparison of arthropod communities between an actively restored post-mining forest, a dominant alternative land-use type (agroforestry plantation), a natural reference (natural forest) and an unmanaged former mining area (gravel mine) provides the first assessment of the effects of land-use decisions in former mining areas in Western Africa on arthropod communities. The observed pronounced differences between communities at a relatively coarse level of taxonomic (order to family) and functional (spider hunting guilds and beetle trophic groups) classification emphasise the need to address these effects in times of global insect decline (Cardoso et al., 2020; Wagner et al., 2021).

Taxonomic composition of arthropod communities

The observed dominance structure in the studied arthropod communities supports our hypothesis that land-use types with diverse and heterogeneous vegetation structure (Tab. 1) support a greater range of arthropod taxa and overall higher activity density (see also Gardner et al., 1995; Mata et al., 2021; Dampney et al., 2022a). The land-use types dominated by trees in this study (natural forest, agroforestry plantation and restored forest) offered additional niches and resources to support the activity of arthropods compared to the un-restored gravel mine. Meloni et al. (2020) showed that even ground-dwelling arthropods benefit from more diverse vegetation and the resulting habitat attributes. Diverse vegetation provides more refuge and protection from predators, resulting in higher survival and reproductive success in potential prey taxa (Wenninger & Inouye, 2008; Zou et al., 2013). For predators, diverse vegetation often correlates with higher prey availability supplying food needs (Schuldt et al., 2011; Staab & Schuldt, 2020; Štokmane & Spunđis, 2016). Deadwood and litter further promote the activity of detritivores, fungivores and arthropod predators that are part of the detritivore food web in forests (Sereda et al., 2012, 2015; Tonin et al., 2018).

Heimonen et al. (2013) emphasised the pronounced seasonal variation of herbivorous insects (e.g. mostly Orthopteroidea) that is common in tropical rain forests. For example, increasing resource concentration in the wet season is a significant factor in determining the population size in specialist herbivore populations (Doublet et al., 2019) and beetle communities (de Castro-Arrazola et al., 2018). The observed differences between the two seasons support our hypothesis that arthropod taxonomic composition is strongly influenced by seasonality across the different land-use types in our study (Lingbeek et al., 2017). Richards and Windsor (2007) observed significant seasonal variation in arthropod abundance in a lowland moist forest. Similarly, Wagner (2001) observed significant seasonal changes in arthropod fauna in a rain forest. Our study observed a higher activity density of Orthoptera (mainly herbivorous) and Polydesmida (mainly detritivorous) in the wet season than in the dry season. Several factors related to macro- and micro-climatic changes (e.g. temperature, rainfall, humidity, day length, decomposition rate of organic materials etc.) might have caused this pattern (Halsch et al., 2021; Wardhaugh et al., 2018; Belchior et al., 2016; Anu et al., 2009). In addition to abiotic conditions, food resources fluctuate seasonally, further affecting arthropod emergence, activity and reproduction (Richards & Windsor, 2007; Silva et al., 2011). Therefore, both structure- and resource-mediated effects likely affected arthropod communities between the seasons (Diehl et al. 2013). Independent of season, arthropod communities changed

along a management intensity gradient in the sequence of agroforestry plantations to actively restore to natural forest arthropod communities. Therefore, the restored communities hold an intermediate position between the plantations and natural forests.

Spider families and hunting guilds

Similar to arthropod communities in general, spider communities are affected by vegetation structure, the presence of potential prey, as well as changes in abiotic conditions (Müller et al., 2022; Rosa et al., 2018; Yamazaki et al., 2017). The restored and natural forests were taxonomically richer than the agroforestry plantation and the gravel site, reflecting the various ecological niches that forest ecosystems provide to arthropods (Rosa et al., 2018). Generally, more complex vegetation offers a wider range of prey (e.g. Diehl et al., 2013) as well as more diverse niches for spiders (Cardoso et al., 2011; Stańska et al., 2018). The observed higher activity density of spiders in the wet season results from precipitation, which drives plant growth as food for insects acting as prey for spiders (Rodríguez-Rodríguez et al., 2015). Spiders that construct sensing webs had higher activity densities in the land-use types dominated by trees resulting from the higher vegetation density and availability of web sites (see Pinto et al., 2021). Balfour and Rypstra (1998) emphasised the role of habitat structure for web support and the availability of suitable microhabitats for web-building spiders. Ambush hunters also had a higher activity density in land-use types that were dominated by trees. Ambush hunters (e.g. Thomisidae) often hide in flowers or on leaves to catch prey (Heiling et al., 2006; Willemart & Lacava, 2017) and, therefore, also rely on vegetation structure.

Beetle families and trophic groups

The activity density of beetles even differed between the three land-use types with trees, with the restored forest (dominated by non-native tree species, e.g. *Tectona grandis*, *Senna siamiae*) recording lower activity densities than the agroforestry plantation and the natural forest. This trend is in line with previous studies that observed a lower beetle diversity in a non-native forest plantation, such as a restored forest, compared to an old-native forest (Fischer & Lindenmayer, 2007). This pattern could be attributed to the fact that younger restored forests still support fewer tree species with limited ability to offer food and niches compared to forests of intermediate age (Lachat et al., 2012).

Moreover, the lower activity density of beetles in the open gravel site could be attributed to the absence or limited availability of suitable habitats and food resources

(Perry et al., 2016). The family Cetoniidae associated with the land-use types with trees has feeding preferences for plant tissues, exudates and organic materials (deadwood) (Mudge et al., 2012), which characterised the forest plots in this study. The higher activity density of Cetoniidae in the tree land-use types could be due to the potential existence of numerous ant colonies (not quantified in this study) for which several species of Cetoniidae are predators (Holm & Marais, 1992). Expectedly, most beetle families showed higher activity density in the wet than in the dry season, in line with previous studies documenting higher diversities of beetles compared to the dry season (Andresen, 1999; Nyeko, 2009) and often attributed to the higher quality and quantity of food resources in the wet season (Wardhaugh et al., 2018).

Similar to the activity density of arthropods, all trophic groups of beetles classified in this study showed significantly higher activity density in the “tree” land-use types than in the “open” gravel site affirming the positive relationship between beetle functional groups and high vegetation structure (Dampney et al., 2022a; Sattler et al., 2010). Trophic groups such as detritivores (Mestre et al., 2018; Parisi et al., 2018; Wende et al., 2017) or herbivores (O'Brien et al., 2017) may have benefited from resources and habitat conditions provided by deadwood and leaf litter in the land-use types with trees. Similar to spiders, predaceous beetles may have also benefited from the higher prey availability in these land-use types (Dampney et al., 2021; Diehl et al., 2013).

Conclusion

The studied active forest restoration shows some promise in moving arthropod communities towards states observed in the natural forest, but arthropod communities in the agroforestry plantations were already more dissimilar. The patterns in arthropod communities observed for the land-use types depended on seasons, with the wet season making essential resources available for arthropods. Leaving former mining sites unmanaged is not a promising option, as arthropod communities and their habitat resource requirements were poor in the gravel site compared to the restored and natural reference forest and even the agroforestry plantation. We recommend that restoration activities in degraded post-mining regions of Ghana should focus on using mostly native tree species since they have the ability to supply habitat and food resources tailored to the needs of local biodiversity.

Appendix 1

See Table 4.

Table 4 Number of individual arthropod order/suborder for land-use types (RF, restored forest; AF, agroforestry plantation; NF, natural forest and GS, gravel site) and seasons (DS, dry; WS, wet)

| Order/suborder | Land-use types | | | | Seasons | |
|----------------|----------------|------|--------|------|---------|--------|
| | RF | AF | NF | GS | DS | WS |
| Acari | 83 | 27 | 176 | 0 | 102 | 184 |
| Araneae | 984 | 567 | 1064 | 477 | 1173 | 1919 |
| Blattodea | 366 | 208 | 1276 | 0 | 784 | 1066 |
| Coleoptera | 1330 | 1555 | 2656 | 223 | 1400 | 4364 |
| Glomerida | 701 | 123 | 682 | 14 | 421 | 1099 |
| Hemiptera | 189 | 195 | 359 | 109 | 616 | 236 |
| Hymenoptera | 7098 | 4471 | 7979 | 2042 | 8716 | 12,874 |
| Julida | 261 | 336 | 409 | 0 | 453 | 553 |
| Opiliones | 13 | 6 | 21 | 0 | 0 | 40 |
| Orthoptera | 2299 | 1629 | 1502 | 1709 | 3103 | 4036 |
| Polydesmida | 69 | 90 | 35 | 7 | 0 | 201 |
| Ricinulei | 5 | 2 | 4 | 0 | 0 | 11 |
| Scolopendra | 1 | 0 | 1 | 0 | 0 | 2 |
| Scorpiones | 4 | 2 | 5 | 0 | 0 | 11 |
| Total | 13,403 | 9211 | 16,169 | 4581 | 16,768 | 26,596 |

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states no conflict of interest.

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References

- Andresen, E. (1999). Seed dispersal by monkeys and the fate of dispersed seeds in a Peruvian Rain Forest. *Biotropica*, *31*, 145. <https://doi.org/10.2307/2663968>
- Asare, D., Ansong, M., Kyereh, B., Dampney, F. G., & Asante, W. (2022). Mining methods exert differential effects on species recruitment at artisanal small-scale mining sites in Ghana. *Heliyon*, *8*, e09434. <https://doi.org/10.1016/j.heliyon.2022.e09434>
- Balfour, R. A., & Rypstra, A. L. (1998). The influence of habitat structure on spider density in a no-till soybean agroecosystem. *Journal of Arachnology*, *26*, 221–226.
- Basset, Y., Cizek, L., Cuénoud, P., Didham, R., Novotny, V., Ødegaard, F., Roslin, T., Tishechkin, A., Schmidl, J., Winchester, N., Roubik, D., Aberlenc, H., Bail, J., Barrios, H., Bridle, J., Castaño-Meneses, G., Corbara, B., Curletti, G., Duarte da Rocha, W., ... Leponce, M. (2015). Arthropod distribution in a tropical rainforest: Tackling a four dimensional puzzle. *PLoS ONE*, *10*, e0144110. <https://doi.org/10.1371/journal.pone.0144110>
- Biondi, M., Urbani, F., & D'Alessandro, P. (2015). Relationships between the geographic distribution of phytophagous insects and different types of vegetation: A case study of the flea beetle genus *Chaetocnema* (Coleoptera: Chrysomelidae) in the Afrotropical region. *European Journal of Entomology*, *112*, 311–327. <https://doi.org/10.14411/eje.2015.040>
- Birkhofer, K., Andersson, G., Bengtsson, J., Bommarco, R., Dänhardt, J., Ekblom, B., Ekroos, J., Hahn, T., Hedlund, K., Jönsson, A., Lindborg, R., Olsson, O., Rader, R., Rusch, A., Stjernman, M., Williams, A., & Smith, H. (2018). Relationships between multiple biodiversity components and ecosystem services along a landscape complexity gradient. *Biological Conservation*, *218*, 247–253. <https://doi.org/10.1016/j.biocon.2017.12.027>

- Birkhofer, K., Smith, H., Weisser, W., Wolters, V., & Gossner, M. (2015). Land-use effects on the functional distinctness of arthropod communities. *Ecography*, *38*, 889–900. <https://doi.org/10.1111/ecog.01141>
- Cardoso, P., Barton, P., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C., Gaigher, R., Habel, J., Hallmann, C., Hill, M., Hochkirch, A., Kwak, M., Mammola, S., Ari Noriega, J., Orfinger, A., Pedraza, F., Pryke, J., Roque, F., ... Samways, M. (2020). Scientists' warning to humanity on insect extinctions. *Biological Conservation*, *242*, 108426. <https://doi.org/10.1016/j.biocon.2020.108426>
- Cardoso, P., Pekár, S., Jocqué, R., & Coddington, J. (2011). Global patterns of guild composition and functional diversity of spiders. *PLoS ONE*, *6*, e21710. <https://doi.org/10.1371/journal.pone.0021710>
- Clarke, K. R., & Gorley, R. N. (2015). *Getting started with PRIMER v7. PRIMER-E*. Plymouth: Plymouth Marine Laboratory.
- Clarke, K. R., Gorley, R. N., Somerfield, P. J., & Warwick, R. M. (2014). *Change in marine communities: An approach to statistical analysis and interpretation* (3rd ed.). PRIMER-E Ltd.
- Culliney, T. (2013). Role of arthropods in maintaining soil fertility. *Agriculture*, *3*, 629–659. <https://doi.org/10.3390/agriculture3040629>
- Dampney, F. G., Birkhofer, K., Nsiah, P., & de la Riva, E. (2020). Soil properties and biomass attributes in a former gravel mine area after two decades of forest restoration. *Land*, *9*, 209. <https://doi.org/10.3390/land9060209>
- Dampney, F. G., Birkhofer, K., Oliveras Menor, I., & de la Riva, E. (2022a). The functional structure of tropical plant communities and soil properties enhance ecosystem functioning and multifunctionality in different ecosystems in Ghana. *Forests*, *13*, 297. <https://doi.org/10.3390/f13020297>
- Dampney, F. G., de la Riva, E., & Birkhofer, K. (2021). Trade-offs and synergies between food and fodder production and other ecosystem services in an actively restored forest, natural forest and an agroforestry system in Ghana. *Frontiers in Forests and Global Change*. <https://doi.org/10.3389/ffgc.2021.630959>
- Dampney, F. G., Frimpong, B., Debrah, D., Agro, P., & Wiafe, E. (2022b). Vegetation attributes drive the taxonomic richness and functional composition of beetles and spiders in mountainous urban green spaces. *Energy, Ecology and Environment*, *7*, 268–280. <https://doi.org/10.1007/s40974-021-00236-z>
- Dangles, O., & Casas, J. (2019). Ecosystem services provided by insects for achieving sustainable development goals. *Ecosystem Services*, *35*, 109–115. <https://doi.org/10.1016/j.ecoser.2018.12.002>
- de Castro-Arrazola, I., Hortal, J., Moretti, M., & Sánchez-Piñero, F. (2018). Spatial and temporal variations of aridity shape dung beetle assemblages towards the Sahara desert. *PeerJ*, *6*, e5210. <https://doi.org/10.7717/peerj.5210>
- Diehl, E., Sereda, E., Wolters, V., & Birkhofer, K. (2013). Effects of predator specialisation, host plant and climate on biological control of aphids by natural enemies: A meta-analysis. *Journal of Applied Ecology*, *50*, 262–270. <https://doi.org/10.1111/1365-2664.12032>
- Dippenaar-Schoeman AS, Jocqué R (1997) African spiders: an identification manual. Plant Protection Research Institute. Handbook No. 9. Agricultural Research Council of South Africa, Pretoria. iv + 392 pp
- Doublet, V., Gidoïn, C., Lefèvre, F., & Boivin, T. (2019). Spatial and temporal patterns of a pulsed resource dynamically drive the distribution of specialist herbivores. *Scientific Reports*. <https://doi.org/10.1038/s41598-019-54297-6>
- Fischer, J., & Lindenmayer, D. B. (2007). Landscape modification and habitat fragmentation: A synthesis. *Global Ecology and Biogeography*, *16*(3), 265–280. <https://doi.org/10.1111/j.1466-8238.2007.00287.x>
- Gagnarli, E., Valboa, G., Vignozzi, N., Goggioli, D., Guidi, S., Tarchi, F., Corino, L., & Simoni, S. (2021). Effects of land-use change on soil functionality and biodiversity: Toward sustainable planning of new vineyards. *Land*, *10*, 358. <https://doi.org/10.3390/land10040358>
- Gardner, S., Cabido, M., Valladares, G., & Diaz, S. (1995). The influence of habitat structure on arthropod diversity in Argentine semi-arid Chaco forest. *Journal of Vegetation Science*, *6*, 349–356. <https://doi.org/10.2307/3236234>
- Greenslade, P. J. M. (1964). Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology*, *33*, 301–310.
- Heiling, A. M., Cheng, K., & Herberstein, M. E. (2006). Picking the right spot: Crab spiders position themselves on flowers to maximise prey attraction. *Behaviour*, *143*, 957–968. <https://doi.org/10.1163/156853906778623662>
- Heimonen, K., Lwanga, J. S., Mutanen, M., Nyman, T., & Roininen, H. (2013). Spatial and temporal variation in community composition of herbivorous insects on *Neoboutonia macrocalyx* in a primary tropical rain forest. *Journal of Tropical Ecology*, *29*, 229–241. <https://doi.org/10.1017/S0266467413000151>
- Holm E, Marais E (1992) Fruit Chafers of Southern Africa (Scarabaeidae: Cetoniini); Ekogilde: Hartbeespoort, South Africa, pp 1–326
- Høye, T., & Culler, L. (2018). Tundra arthropods provide key insights into ecological responses to environmental change. *Polar Biology*, *41*, 1523–1529. <https://doi.org/10.1007/s00300-018-2370-x>
- Huberty, A., & Denno, R. (2004). Plant water stress and its consequences for herbivorous insects: A new synthesis. *Ecology*, *85*, 1383–1398. <https://doi.org/10.1890/03-0352>
- Isaacs, R., Tuell, J., Fiedler, A., Gardiner, M., & Landis, D. (2009). Maximising arthropod-mediated ecosystem services in agricultural landscapes: The role of native plants. *Frontiers in Ecology and the Environment*, *7*, 196–203. <https://doi.org/10.1890/080035>
- Lachat, T., Wermelinger, B., Gossner, M., Bussler, H., Isacsson, G., & Müller, J. (2012). Saproxyllic beetles as indicator species for deadwood amount and temperature in European beech forests. *Ecological Indicators*, *23*, 323–331. <https://doi.org/10.1016/j.ecoli.2012.04.013>
- Lassau, S. A., Hochuli, D., Cassis, G., & Reid, C. (2005). Effects of habitat complexity on forest beetle diversity: Do functional groups respond consistently? *Diversity and Distributions*, *11*, 73–82. <https://doi.org/10.1111/j.1366-9516.2005.00124.x>
- Lingbeek, B. J., Higgins, C., Muir, J., Kattes, D., & Schwertner, T. (2017). Arthropod diversity and assemblage structure response to deforestation and desertification in the Sahel of western Senegal. *Global Ecology and Conservation*, *11*, 165–176. <https://doi.org/10.1016/j.gecco.2017.06.004>
- Mata, L., Andersen, A., Morán-Ordóñez, A., Hahs, A., Backstrom, A., Ives, C., Bickel, D., Duncan, D., Palma, E., Thomas, F., Cranney, K., Walker, K., Shears, I., Semeraro, L., Malipatil, M., Moir, M., Plein, M., Porch, N., Vesk, P., ... Lynch, Y. (2021). Indigenous plants promote insect biodiversity in urban greenspaces. *Ecological Applications*. <https://doi.org/10.1002/eap.2309>
- May, R. (2010). Tropical arthropod species, more or less? *Science*, *329*, 41–42. <https://doi.org/10.1126/science.1191058>
- Meloni, F., Civieta, B. F., Zaragoza, J. A., Lourdes Moraza, M., & Bautista, S. (2020). Vegetation pattern modulates ground arthropod diversity in semi-arid mediterranean steppes. *Insects*, *11*, 59. <https://doi.org/10.3390/insects11010059>
- Mestre, L., Jansson, N., & Ranius, T. (2018). Saproxyllic biodiversity and decomposition rate decrease with small-scale isolation of tree hollows. *Biological Conservation*, *227*, 226–232. <https://doi.org/10.1016/j.biocon.2018.09.023>

- Millard, J., Outhwaite, C., Kinnersley, R., Freeman, R., Gregory, R., Adedjoja, O., Gavini, S., Kioko, E., Kuhlmann, M., Ollerton, J., Ren, Z., & Newbold, T. (2021). Global effects of land-use intensity on local pollinator biodiversity. *Nature Communications*. <https://doi.org/10.1038/s41467-021-23228-3>
- Mudge, A. D., Orozco, J., Keith Philips, T., & Antoine, P. (2012). The cetoniine fauna of the Upper Guinean forests and savannas of Ghana (Coleoptera: Scarabaeidae: Cetoniinae). *Terrestrial Arthropod Reviews*, 5, 113–174. <https://doi.org/10.1163/187498312x635319>
- Müller, J., Brandl, R., Cadotte, M., Heibl, C., Bässler, C., Weiß, I., Birkhofer, K., Thorn, S., & Seibold, S. (2022). A replicated study on the response of spider assemblages to regional and local processes. *Ecological Monographs*. <https://doi.org/10.1002/ecm.1511>
- Newbold, T. (2018). Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. *Proceedings of the Royal Society b: Biological Sciences*, 285, 20180792. <https://doi.org/10.1098/rspb.2018.0792>
- Novotny, V., Basset, Y., Miller, S., Weiblen, G., Bremer, B., Cizek, L., & Drozd, P. (2002). Low host specificity of herbivorous insects in a tropical forest. *Nature*, 416, 841–844. <https://doi.org/10.1038/416841a>
- Nyeko, P. (2009). Dung beetle assemblages and seasonality in primary forest and forest fragments on agricultural landscapes in Budongo, Uganda. *Biotropica*, 41, 476–484. <https://doi.org/10.1111/j.1744-7429.2009.00499.x>
- Nyffeler, M., Olson, E., & Symondson, W. (2016). Plant-eating by spiders. *Journal of Arachnology*, 44, 15–27. <https://doi.org/10.1636/p15-45.1>
- O'Brien, M., Brezzi, M., Schuldt, A., Zhang, J., Ma, K., Schmid, B., & Niklaus, P. (2017). Tree diversity drives diversity of arthropod herbivores, but successional stage mediates detritivores. *Ecology and Evolution*, 7, 8753–8760. <https://doi.org/10.1002/ece3.3411>
- Ødegaard, F. (2000). How many species of arthropods? Erwin's estimate revised. *Biological Journal of the Linnean Society*, 71, 583–597. <https://doi.org/10.1111/j.1095-8312.2000.tb01279.x>
- Ofofu, G., Dittmann, A., Sarpong, D., & Botchie, D. (2020). Socio-economic and environmental implications of Artisanal and Small-scale Mining (ASM) on agriculture and livelihoods. *Environmental Science & Policy*, 106, 210–220. <https://doi.org/10.1016/j.envsci.2020.02.005>
- Ontl, T., Janowiak, M., Swanson, C., Daley, J., Handler, S., Cornett, M., Hagenbuch, S., Handrick, C., McCarthy, L., & Patch, N. (2020). Forest management for carbon sequestration and climate adaptation. *Journal of Forestry*, 118, 86–101. <https://doi.org/10.1093/jofore/fvz062>
- Owusu, K., & Waylen, P. (2012). The changing rainy season climatology of mid-Ghana. *Theoretical and Applied Climatology*, 112, 419–430. <https://doi.org/10.1007/s00704-012-0736-5>
- Parisi, F., Pioli, S., Lombardi, F., Frivolini, G., Marchetti, M., & Tognetti, R. (2018). Linking deadwood traits with saproxylic invertebrates and fungi in European forests—A review. *iForest—Biogeosciences and Forestry*, 11, 423–436. <https://doi.org/10.3832/ifer2670-011>
- Perner, J., & Schueler, S. (2004). Estimating the density of ground-dwelling arthropods with pitfall traps using a nested-cross array. *Journal of Animal Ecology*, 73, 469–477. <https://doi.org/10.1111/j.0021-8790.2004.00821.x>
- Perry, J., Lojka, B., Quinones Ruiz, L., Van Damme, P., Houška, J., & Fernandez Cusimamani, E. (2016). How natural forest conversion affects insect biodiversity in the Peruvian Amazon: Can agroforestry help? *Forests*, 7, 82. <https://doi.org/10.3390/f7040082>
- Picanço, A., Rigal, F., Matthews, T., Cardoso, P., & Borges, P. (2017). Impact of land-use change on flower-visiting insect communities on an oceanic island. *Insect Conservation and Diversity*, 10, 211–223. <https://doi.org/10.1111/icad.12216>
- Picker, M. (2012). *Field guide to insects of South Africa*. Penguin Random House.
- Pinto, C., Pairo, P., Bellocq, M., & Filloy, J. (2021). Different land-use types equally impoverish but differentially preserve grassland species and functional traits of spider assemblages. *Scientific Reports*. <https://doi.org/10.1038/s41598-021-89658-7>
- R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing. ISBN 3-900051-07-0
- Rader, R., Bartomeus, I., Garibaldi, L., Garratt, M., Howlett, B., Winfree, R., Cunningham, S., Mayfield, M., Arthur, A., Anderson, G., Bommarco, R., Brittain, C., Carvalheiro, L., Chacoff, N., Entling, M., Foully, B., Freitas, B., Gemmill-Herren, B., Ghazoul, J., ... Woyciechowski, M. (2016). Non-bee insects are important contributors to global crop pollination. *Proceedings of the National Academy of Sciences*, 113, 146–151. <https://doi.org/10.1073/pnas.1517092112>
- Richards, L., & Windsor, D. (2007). Seasonal variation of arthropod abundance in gaps and the understorey of a lowland moist forest in Panama. *Journal of Tropical Ecology*, 23, 169–176. <https://doi.org/10.1017/s0266467406003907>
- Rodríguez-Rodríguez, S., Solís-Catalán, K., & Valdez-Mondragón, A. (2015). Diversity and seasonal abundance of anthropogenic spiders (Arachnida: Araneae) in different urban zones of the city of Chilpancingo, Guerrero, Mexico. *Revista Mexicana De Biodiversidad*, 86, 962–971. <https://doi.org/10.1016/j.rmb.2015.09.002>
- Rosa, M., Santos, J., Brescovit, A., Mafra, Á., & Baretta, D. (2018). Spiders (Arachnida: Araneae) in agricultural land use systems in subtropical environments. *Revista Brasileira De Ciência Do Solo*. <https://doi.org/10.1590/18069657rbc20160576>
- Sagi, N., & Hawlena, D. (2021). Arthropods as the engine of nutrient cycling in arid ecosystems. *InSects*, 12, 726. <https://doi.org/10.3390/insects12080726>
- Sattler, T., Duelli, P., Obrist, M., Arlettaz, R., & Moretti, M. (2010). Response of arthropod species richness and functional groups to urban habitat structure and management. *Landscape Ecology*, 25, 941–954. <https://doi.org/10.1007/s10980-010-9473-2>
- Schowalter, T. (2017). Arthropod diversity and functional importance in old-growth forests of North America. *Forests*, 8, 97. <https://doi.org/10.3390/f8040097>
- Schroeder, H., Grab, H., Kessler, A., & Poveda, K. (2021). Human-mediated land use change drives intraspecific plant trait variation. *Frontiers in Plant Science*. <https://doi.org/10.3389/fpls.2020.592881>
- Schueler, V., Kuemmerle, T., & Schröder, H. (2011). Impacts of surface gold mining on land use systems in Western Ghana. *Ambio*, 40, 528–539. <https://doi.org/10.1007/s13280-011-0141-9>
- Schuldt, A., Both, S., Bruelheide, H., Härdtle, W., Schmid, B., Zhou, H., & Assmann, T. (2011). Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity. *PLoS ONE*, 6, e22905. <https://doi.org/10.1371/journal.pone.0022905>
- Seibold, S., Gossner, M., Simons, N., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J., Linsenmair, K., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E., Vogt, J., Wöllauer, S., & Weisser, W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, 574, 671–674. <https://doi.org/10.1038/s41586-019-1684-3>
- Serada, E., Blick, T., Dorow, W., Wolters, V., & Birkhofer, K. (2012). Spatial distribution of spiders and epedaphic Collembola in an environmentally heterogeneous forest floor habitat. *Pedobiologia*, 55, 241–245. <https://doi.org/10.1016/j.pedobi.2012.03.007>

- Sereda, E., Wolters, V., & Birkhofer, K. (2015). Addition of crop residues affects a detritus-based food chain depending on litter type and farming system. *Basic and Applied Ecology*, *16*, 746–754. <https://doi.org/10.1016/j.baec.2015.07.005>
- Silva, N., Frizzas, M., & Oliveira, C. (2011). Seasonality in insect abundance in the “Cerrado” of Goiás State, Brazil. *Revista Brasileira De Entomologia*, *55*, 79–87. <https://doi.org/10.1590/s0085-56262011000100013>
- Somerfield, P., & Clarke, K. (2013). Inverse analysis in non-parametric multivariate analyses: Distinguishing groups of associated species which covary coherently across samples. *Journal of Experimental Marine Biology and Ecology*, *449*, 261–273. <https://doi.org/10.1016/j.jembe.2013.10.002>
- Sonter, L., Ali, S., & Watson, J. (2018). Mining and biodiversity: Key issues and research needs in conservation science. *Proceedings of the Royal Society b: Biological Sciences*, *285*, 20181926. <https://doi.org/10.1098/rspb.2018.1926>
- Staab, M., & Schuldt, A. (2020). The influence of tree diversity on natural enemies—A review of the “enemies” hypothesis in forests. *Current Forestry Reports*, *6*, 243–259. <https://doi.org/10.1007/s40725-020-00123-6>
- Stańska, M., Stański, T., Wielgosz, E., & Hajdamowicz, I. (2018). Impact of habitat complexity on body size of two spider species, *Alopecosa cuneata* and *A. pulverulenta* (Araneae, Lycosidae), in River Valley Grasslands. *Polish Journal of Environmental Studies*, *27*, 853–859. <https://doi.org/10.15244/pjoes/75806>
- Štokmane, M., & Spuņģis, V. (2016). The influence of vegetation structure on spider species richness, diversity and community organisation in the *Apšuciems calcareous* fen, Latvia. *Animal Biodiversity and Conservation*, *39*, 221–236. <https://doi.org/10.32800/abc.2016.39.0221>
- Stork, N. (2018). How many species of insects and other terrestrial arthropods are there on earth? *Annual Review of Entomology*, *63*, 31–45. <https://doi.org/10.1146/annurev-ento-020117-043348>
- Stuart, S. N., Adams, R. J., & Jenkins, M. (1990). Biodiversity in sub-Saharan Africa and its islands: Conservation, management, and sustainable use. *Occasional Paper of the IUCN Species Survival Commission*, *6*, 1–242.
- Tonin, A., Pozo, J., Monroy, S., Basaguren, A., Pérez, J., Gonçalves, J., Pearson, R., Cardinale, B., & Boyero, L. (2018). Interactions between large and small detritivores influence how biodiversity impacts litter decomposition. *Journal of Animal Ecology*, *87*, 1465–1474. <https://doi.org/10.1111/1365-2656.12876>
- Underwood, E., & Quinn, J. (2010). Response of ants and spiders to prescribed fire in oak woodlands of California. *Journal of Insect Conservation*, *14*, 359–366. <https://doi.org/10.1007/s10841-010-9265-7>
- van der Sluijs, J., & Vaage, N. (2016). Pollinators and global food security: The need for holistic global stewardship. *Food Ethics*, *1*, 75–91. <https://doi.org/10.1007/s41055-016-0003-z>
- Wagner, D., Grames, E., Forister, M., Berenbaum, M., & Stopak, D. (2021). Insect decline in the anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Sciences*. <https://doi.org/10.1073/pnas.2023989118>
- Wagner, T. (2001). Seasonal changes in the canopy arthropod fauna in *Rinorea beniensis* in Budongo Forest, Uganda. *Tropical Forest Canopies: Ecology and Management*. https://doi.org/10.1007/978-94-017-3606-0_13
- Wardhaugh, C., Stone, M., & Stork, N. (2018). Seasonal variation in a diverse beetle assemblage along two elevational gradients in the Australian Wet Tropics. *Scientific Reports*. <https://doi.org/10.1038/s41598-018-26216-8>
- Wende, B., Gossner, M., Grass, I., Arnstadt, T., Hofrichter, M., Floren, A., Linsenmair, K., Weisser, W., & Steffan-Dewenter, I. (2017). Trophic level, successional age and trait matching determine specialisation of deadwood-based interaction networks of saproxylic beetles. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20170198. <https://doi.org/10.1098/rspb.2017.0198>
- Weninger, E., & Inouye, R. (2008). Insect community response to plant diversity and productivity in a sagebrush–steppe ecosystem. *Journal of Arid Environments*, *72*, 24–33. <https://doi.org/10.1016/j.jaridenv.2007.04.005>
- Willemart, R. H., & Lacava, M. (2017). Foraging strategies of cursorial and ambush spiders. In C. Viera & M. O. Gonzaga (Eds.), *Behaviour and ecology of spiders* (pp. 227–245). Springer. <https://doi.org/10.1007/978-3-319-65717-2>
- Yamazaki, L., Vindica, V., Brescovit, A., Marques, M., & Battistola, L. (2017). Temporal variation in the spider assemblage (Arachnida, Araneae) in canopies of *Callisthene fasciculata* (Vochysiaceae) in the Brazilian Pantanal biome. *Iheringia. Série Zoologia*. <https://doi.org/10.1590/1678-4766e2017019>
- Zou, Y., Sang, W., Bai, F., & Axmacher, J. (2013). Relationships between plant diversity and the abundance and α -diversity of predatory ground beetles (Coleoptera: Carabidae) in a mature Asian temperate forest ecosystem. *PLoS ONE*, *8*, e82792. <https://doi.org/10.1371/journal.pone.0082792>