

A META-FOOD WEB FOR INVERTEBRATE SPECIES COLLECTED IN A EUROPEAN GRASSLAND

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INTRODUCTION

METADATA

CLASS I. DATA SET DESCRIPTORS

A. Data set identity: Meta-food web data set of species traits (Jena species traits) and potential trophic interactions (Jena trophic interactions) among 714 grassland invertebrate species and their food resources

B. Data set identification code:

- 1) Jena species traits: Jena_species_traits.csv
- 2) Jena trophic interactions: Jena_trophic_interactions.csv.

C. Data set description

1. Originators

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2. Abstract

Patterns of feeding interactions between species are thought to influence the stability of communities and the flux of nutrients and energy through ecosystems. However, surprisingly few well-resolved food webs allow us to evaluate factors that influence the architecture of species interactions. We constructed a meta-food web consisting of 714 invertebrate species collected over nine years of suction and pitfall sampling campaigns in the Jena Experiment, a long-term grassland biodiversity experiment located in Jena, Germany. In this paper, we summarize information on the 51,496 potential trophic links, which were established using information on diet specificity and species traits that typically constrain feeding interactions (trophic group, body size, and vertical stratification). The list of species identities, traits, and

link-derivation rules will be useful not only for tests of plant diversity effects on food web structure within the Jena Experiment, but also for considering consistent construction of food webs from empirical data, and for comparisons of network structure across ecosystems. No copyright or proprietary restrictions are associated with the use of this data set other than citation of this Data Paper.

D. Keywords:

Meta-matrix, food web, trophic interactions, grassland, invertebrate, species traits

CLASS II. RESEARCH ORIGIN DESCRIPTORS

A. Overall project description

1. Identity Consumer food web structure in diverse grasslands

2. Originators: Jes Hines, Darren P. Giling, Michael Rzanny, Winfried Voigt, Sebastian T. Meyer, Wolfgang W. Weisser, Nico Eisenhauer, Anne Ebeling

3. Period of study 2003-2012

4. Objectives:

A central focus of contemporary ecology is to document and predict ecosystem responses to environmental change (IPCC 2014). Some of the most prominent responses taking place include changes in the biological diversity of communities (Walther et al. 2002, Parmesan and Yohe 2003). Widespread interest in how biodiversity changes will propagate across communities by altering species interactions has prompted scientists to study topological food webs that document the presence and patterns of feeding interactions in communities (Dunne et al. 2002, Delmas et al. 2018). For example, empirical work has revealed characteristic regularities in the patterns of species interactions across ecosystems (Riede et al. 2010). That is, nature has particular architectural styles that we see over and over again (Thébault and Fontaine 2010). Subsequent work, using both empiricism and theory, has sought to understand how the composition of communities, and the complexity of their interactions, influence the stability, assembly and disassembly of food webs (Bascompte and Stouffer 2009, Fahimipour and Hein 2014).

Although scientists have studied the structure, dynamics, and stability of food webs since the early 1900s (Elton 2001), why characteristic patterns in food webs emerge is still not exactly clear. This is, in part, because well-resolved food webs for particular habitats are still not common. Additionally, it is challenging to compare existing food webs across environments when they have been compiled using different criteria to establish presence of species and their feeding interactions. To address these data limitations, researchers are compiling databases consisting of replicate food webs for particular systems across various kinds of gradients (Tylianakis and Morris 2017, Pellissier et al. 2018). These databases are often formed by constructing meta-food webs, that is, master webs containing all species collected or observed and all potential feeding links that would be realized if species sampled across the gradients were to co-occur (Pascual and Dunne 2006). Published meta-webs of species interactions encourage scientists to establish links in a consistent fashion, allowing for databases of networks following consistent protocols. Considered together, published meta-webs and their companion studies documenting food web responses to environmental gradients will provide compelling new insights into the causes and consequences of interaction complexity (Hines et al. 2015).

Given that individuals interact with each other in complex ways that are often difficult to observe, all food webs necessarily reflect abstractions designed to portray the essential essence of trophic interactions. Yet, defining consistently meaningful differences in diets across large numbers of species, has proven difficult (Woodward et al. 2005, Eklöf et al. 2013b, Roslin and Majaneva 2016). Moving from a completely unresolved network, where all species could consume each other, to a well-resolved food web with a reasonable degree of realism requires one to integrate taxonomic and trait-based information using a set of simplifying assumptions (Fig. 1). One approach is to consider coarse trophic groups (plant/resource, herbivore, detritivore omnivore, predator), which can indicate fundamental forbidden links (i.e. plants typically do not eat predators). As invertebrates at higher trophic levels typically contain more nitrogen than the resources they consume (Martinson et al. 2008), even this crude trophic resolution can result in important insights into nutrient and energy fluxes (Elser and Urabe 1999, González et al. 2017).

Additionally, taxonomy, observations, and trait-based information can further resolve potential links, according to link-derivation rules (Table 1). Similar feeding link rules are broadly applied to describe potential diets of many different organisms in both terrestrial and aquatic realms (Pauly et al. 2000, Christensen and Walters 2004), and they allow for increased transparency in how links are designated (Bartomeus et al. 2016). For example, in intensively studied systems like European grasslands, peer reviewed manuscripts (Nickel 2003), books

(Southwood and Leston 1959), and reputable online databases provide reliable information on diets of consumer species that feed on particular host plants (link type 1), taxonomic groups (link type 2), or trophic groups (link type 3). Matching traits of consumers with traits of their potential resources is a good predictor of the presence of trophic interactions for generalist species that consume a wide range of prey species (Bartomeus et al. 2016, Laigle et al. 2018). For example, when consumer or resource taxa have strong affinity for particular habitats (i.e. ground-dwelling, web-spinning spiders), taxonomy and shared micro-habitat preferences are strong predictors of trophic interactions (link type 4) (Bartomeus et al. 2016). Simultaneously matching multiple traits of consumers and their resources has been shown to accurately capture the majority of feeding interactions of generalist taxa (link type 5) (Eklöf et al. 2013a, Laigle et al. 2018). Considered together, the link-derivation rules capture a wide range of potential diet types, allowing us to consider not only how diversity changes may influence the species present in a community, but also how those changes may alter the structure and stability of food webs.

Table 1. Link-derivation rules.

Link type	Description	Example (number of links in Jena meta-food web)
1	Specific feeding interaction reported in the literature	Taxa known to feed on a specific species that is present in the Jena Experiment. This type of link is most commonly applied for monophagous herbivores. For example, <i>Ditropsis flavipes</i> (Delphacidae: Hemiptera) is monophagous on <i>Bromus erectus</i> (Remane and Washmann 1993, Nickel 2003). (1,126 links)
2	Generalized feeding interaction reported in the literature	Taxa that are reported to feed on all species in a given taxonomic group. This type of interaction is typical for oligophagous and polyphagous herbivores. For example, <i>Chrysolina oricalcia</i> (Chrysomelidae: Coleoptera) is oligophagous, commonly feeding on plants in the family Apiaceae (Cox 2007). (3,669 links)
3	Trophic level	Taxa feed on resources based on trophic group. For example, <i>Megalonotus chiragra</i> (Lygaeidae: Hemiptera) is a generalist

		herbivore that feeds on the seeds of plants (Eyles 1964, Wachmann et al. 2008). (2,872 links)
4	Trait-based rule	Links based on taxonomic identity and matching single trait such as vertical stratification of consumer and resource. For example, <i>Coelotes terrestris</i> is a large spider, whose webs typically catch non-spider prey that forage at the ground level (Nyffeler and G. 1989, Nyffeler et al. 1994). (9,701 links)
5	Combined trait-based rules	5.1 Links based on taxa, body size, vertical stratification. This link is common for generalist spiders and rove beetles. Due to constraints in foraging and handling time, predators like <i>Pardosa palustris</i> typically feed on prey that are 20-80% of their body size, and found in overlapping vertical distribution (Nyffeler et al. 1994, Ubick et al. 2004, Bellman 2010). (25,319 links)
		5.2 Links based on taxa, body size, and trophic level of consumers and resources. Link most common for polyphagous omnivorous carabid beetles that feed on prey across levels of vertical stratification throughout their lives (Hengeveld 1980). (7,195 links)
		5.3 Links based on taxa, body size, vertical stratification, and trophic level. This link type is most common for intermediate predators. For example, <i>Propylea quatuordec</i> (Coccinellidae: Coleoptera) typically feeds on smaller herbivorous hemipterans in the herbaceous vegetation (Kalushov and Hodek 2005). (851 links)
		5.4 Links based on taxa, larger body size range restriction, trophic level, and vertical stratification. Piercing predators with extra-oral digestion are able to capture prey with a slightly broader range (20-120%) of body sizes. For example, <i>Nabis brevis</i> (Nabidae, Hemiptera) can feed on herbivorous prey with a broad range of sizes (Lattin 1989). (763 links)

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B. Specific project description

1. Site description

The list of consumers and resources (Jena species traits) in the meta-matrix presented here (Jena trophic interactions) were populated based on the pool of species sown and consistently sampled in the Jena Experiment, a plant-diversity experiment established in 2002 in Jena, Germany (50 ° 55 ' N, 11 ° 35 ' E; 130 m a.s.l.) (Roscher et al. 2004).

2. Experimental design

a. Design characteristics

Resources consist of the 60 plant species native to central European grasslands, which originally were sown into 20 x 20 m plots to establish plant communities composed of 1, 2, 4, 8, 16 or 60 species. In 2009, the plot size was reduced to 100 m², the plot shape was changed from one square to two connected rectangles, and two of the monocultures were abandoned due to poor cover of the target species. Plots are arranged in four spatial blocks designed to control for spatial variation in soil texture (Roscher et al. 2004). Ubiquitous grassland resources (detritus, microbes, algae, carrion, dung, moss, and fungi) were also included as coarse categories of potential food sources for invertebrate taxa (Hunt et al. 1987, Dindal 1990, de Ruiter et al. 1995).

b. Data collection period and frequency

Ground- and vegetation-associated arthropods were sampled using pitfall (32 sample dates) and suction sampling (14 sample dates) in four years: 2003, 2005, 2010, and 2012 (Supplemental Table 1). For suction samples, a vacuum sampler (Kärcher A2500, Kärcher GmbH, Winnenden, Germany) was used to exhaustively sample vegetation-associated arthropods within a mesh-covered cube frame (surface area 0.75 x 0.75 m) that was randomly placed in five locations in the 20 x 20 m plots (2003, 2005) (Rzanny and Voigt 2012, Rzanny et al. 2013), three locations in 2010 (Ebeling et al. 2018b), and two locations in 2012 (Ebeling et al. 2018a), due to reduction in plots size and increasing workload associated with other aspects of the experiment. In each plot, two pitfall traps (4.5 cm diameter) filled with 3%

formalin were left uncovered for two weeks prior to the pitfall sampling date to collect ground-associated invertebrates (Brook et al. 2008) as reported by (Rzanny and Voigt 2012, Ebeling et al. 2018a, Ebeling et al. 2018b). After collection, invertebrates were stored in 70% ethanol before scientists with expertise in focal taxonomic groups identified individuals to species (Isopoda: Gerlinde Kratzsch, Norman Lindner; Myriapoda: Michael Meyer; Orthoptera: Günter Köhler; Auchenorrhyncha: Roland Achtziger, Heteroptera: Franz Schmolke, Ralk Heckmann; Coleoptera: Eric Anton, Araneae: Theo Blick, Christoph Muster). In 2003 and 2005, samples were collected from plots with plant species richness of 1, 4, 16, and 60, and in subsequent years, invertebrate samples were collected from plots sown with plant species richness of 1, 2, 4, 8, 16, and 60. Taxonomic orders were included if they were consistently sampled and identified across all four years. Species were included in the meta-matrix if more than two individuals were collected in the sampling campaigns conducted in a given year. Including the 60 plant species, 714 species, in 431 genera, 109 families, and 27 orders were collected (Jena species traits; list of nodes Fig. 1). The invertebrate taxa were predominantly Coleoptera, Hemiptera, and Araneae (Fig. 2A).

3. Research Methods:

a) Invertebrate traits

Invertebrate traits (vertical stratum, body size, trophic group) were recorded for each species based on peer-reviewed literature, author's and taxonomist's expertise, field guides, and reputable websites (Rzanny and Voigt 2012, Ebeling et al. 2018b) (Data set 1: Jena species traits; see trait frequencies in Fig. 2B-D). To assess whether species were likely to encounter and feed on each other, we assessed vertical stratification of the habitat as an aspect of spatial niche partitioning. Species were scored as being most commonly associated with ground strata, herbaceous strata, or indifferent to strata by foraging across levels of vertical stratification (Fig. 2B). Body size is reported as average body length (mm) of species (Fig. 2C), as this is an important factor constraining food web structure by influencing predator handling time (Petchey et al. 2008), and this data can be converted to body-mass estimates using length-mass regressions (Gowing and Recher 1984, Sohlstroem et al. 2018). Broad trophic groups were categorized to report an initial assessment of dominant diet tendencies (listed from most- to least-species rich herbivore, predator, omnivore, detritivore; Fig. 2D). These feeding tendencies preferences in weighted networks, or used as a benchmark for comparisons of inferences drawn from other approaches (Rzanny and Voigt 2012, Ebeling et al. 2018a, Ebeling et al. 2018b). In reality, however, predator, detritivore, and omnivore species have a more continuous and taxa-specific range of diet preferences than a coarse trophic grouping might suggest. For example, detritivores and predators often supplement

their diet with prey and detritus respectively, and these additional feeding interactions are captured in the meta-matrix (Data Set 2: Jena trophic interactions).

b) Invertebrate feeding interactions

Invertebrate feeding interactions were established using five link types that reflect a generalizable range of differences in the diet specificity among organisms (Table 1). From link type 1 to link type 5, rules transition from reliance on field observations to reliance on trait-based information. These link types were established based on literature searches, using species names AND “diet”, OR “host plant”, OR “feeding” as search terms, as well as expert knowledge of taxonomists and co-authors (Data Set 1: Jena species traits, Supplemental Table 2). Literature and trait-based food webs reflect potential feeding interactions that are likely to occur when the species co-occur in the given species pool (Morales-Castilla et al. 2015a, Delmas et al. 2018). It is tempting to say that the numbered link-derivation rules could be associated with certainty of any given link. Yet, because these five link types reflect real differences in diet specificity among organisms, any potential changes in the prominence of a given link type necessarily reflect changes in the taxonomic composition of the food web as well as any potential changes in confidence regarding food web structure. This can be visualized by examining the distribution of links derived from each of the rules as depicted on two of the main trait axes (trophic level and vertical stratification) (Fig. 3).

CLASS III. DATA SET STATUS AND ACCESSIBILITY

A. Status

1. Latest update: July 2018

2. Latest Archive data: July 2018

3. Metadata status: Metadata is current and up to date

4. Data verification: All species names were provided by taxonomic experts (see methods) and double-checked and cross-referenced with online databases (i.e. <https://fauna-eu.org/>, and <http://tolweb.org/tree/phylogeny.html>) to check for synonyms and changes in species naming across the sampling campaigns. Contrasting evidence for species’ interactions are sometimes reported, and distinct preferences of generalist taxa are often undocumented or reflect site-specific species pools rather than true diet specialization. Therefore, as noted also by other scientists constructing food webs using similar methods (Martinez 1991), species feeding interactions documented by different methods may result in slightly differing linkages that

would also contribute their own biases (Rzanny and Voigt 2012, Rzanny et al. 2013, Delmas et al. 2018, Ebeling et al. 2018b). Our trait-based rules help to limit the influence of these biases and provide a broadly applicable framework for food web construction. Additionally, we searched for feeding-interaction data for each species individually and used multiple sources in attempt to derive robust trophic-interaction data that could be justified by many cited references (Supplemental Table 2).

B. Accessibility

Storage location and medium: The Ecological Society of America’s journal *Ecology* in the *Data Papers* section

Contact person: Jes Hines, German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Leipzig Germany 04103 (jessica.hines@idiv.de)

Copyright restrictions: None

Proprietary restrictions: None

Costs: None

CLASS IV DATA STRUCTURAL DESCRIPTORS

A. Data Set File

1. Identity: The data set is downloadable as a single zipped archive, DataS1.7z (32KB), which contains the following two files stored as comma-separated values (.csv).

1) Jena_species_traits (94KB): Species traits and literature information (species_traits.csv). The species trait data contains the species code, taxonomic identity, species traits, literature references of the 714 species collected by pitfall and suction sampler in the Jena Experiment. For header information see Table 2.

Table 2: Overview of all variables in species traits data set: “Jena_species_traits.csv”.

Column Heading	Description
species.code	Identification code of species

genus.species	Genus and species name
Kingdom	Taxonomic resolution Kingdom
Phylum	Taxonomic resolution Phylum
Class	Taxonomic resolution Class
Order	Taxonomic resolution Order
Family	Taxonomic resolution Family
Genus	Taxonomic resolution Genus
Species	Taxonomic resolution Species
trophic.group	Coarse trophic group (resource, plant, herbivore, predator, omnivore)
resolution	Taxonomic resolution
size	Body length in mm
vertical.stratum	Vertical distribution of habitat with which the species is associated (g=ground, i=indifferent, h=herb, p=plant species).
feeding.reference.supplemental.table.2	Literature reference for feeding link. Numbers refer to references listed in Supplemental Table 1.
link.type	Link type described in Table 1.

2) Jena_trophic_interactions (1075 KB): The meta-food web data set contains the species code, and link types identifying potential trophic interactions among the 714 species collected by pitfall and suction sampling in the Jena Experiment (Jena_trophic_interactions.csv). For header information see Table 3.

Table 3. Meta data describing content of row names, column names and the data values of the species-level meta-food web for potential trophic interactions among 714 invertebrate species collected in pitfall and suction samples in the Jena Experiment (Jena_trophic_interactions.csv).

Row names	Column names	Data values
Identification code of resource species listed in data citation 1.	Identification code of consumer species listed in data citation 1.	Interactions are given by the numeric code for link type in Table 1. A zero indicates no potential feeding interaction between the two species.

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Author contributions

JH, DG, WV, WWW, NE, AE contributed to conceptualization of the project. WV, WWW, NE, AE led coordination and implementation of the field work. JH, DG, MR, STM, AE collected and compiled the trait and feeding interaction data. JH wrote the manuscript, and all authors approved of the final draft.

Literature Cited

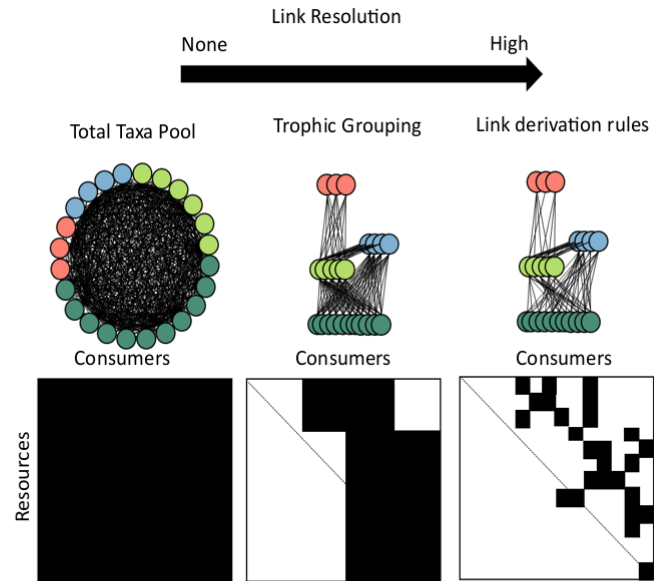
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Taxon resolution	Number of Nodes	Number of Links (Connectance)		
		Species	Genus	Family
Species	714	509,796 (1)	464,957 (0.91)	51,496 (0.10)
Genus	431	185,761 (1)	167,027 (0.90)	19,619 (0.11)
Family	109	11,881 (1)	10,082 (0.85)	1673 (0.14)
Order	27	729 (1)	379 (0.52)	121 (0.17)

Figure 1. Conceptual over-view of the meta-food web constructed using the taxa present in the Jena Experiment. Food-web metrics (number of nodes, number of links, and connectance [links/species²]) can be derived from taxa x taxa food web matrices depending on taxonomic or trophic aggregation. Links can be established from the total taxa pool by considering trophic grouping (colors indicate trophic group plants/resources =green, herbivores= blue, predators=red, and omnivores=purple). Alternatively, information on taxa-specific diets, trophic group, body size, and vertical distribution can be integrated using link type rules (Table 1). Aggregation of nodes and links based on taxonomic resolution (species, genus, family, order) reduces the number of nodes and the precision of feeding interactions. Because resources nodes (i.e. microbes, litter) are ubiquitous and lack the same taxonomic resolution as the other nodes, we group them at the genus level. Aggregation has less influence on connectance when using information for link-derivation rules, than when using trophic grouping approaches, where each taxa is associated with many low-resolution links. Framework for food-web insets inspired by (Morales-Castilla et al. 2015b).

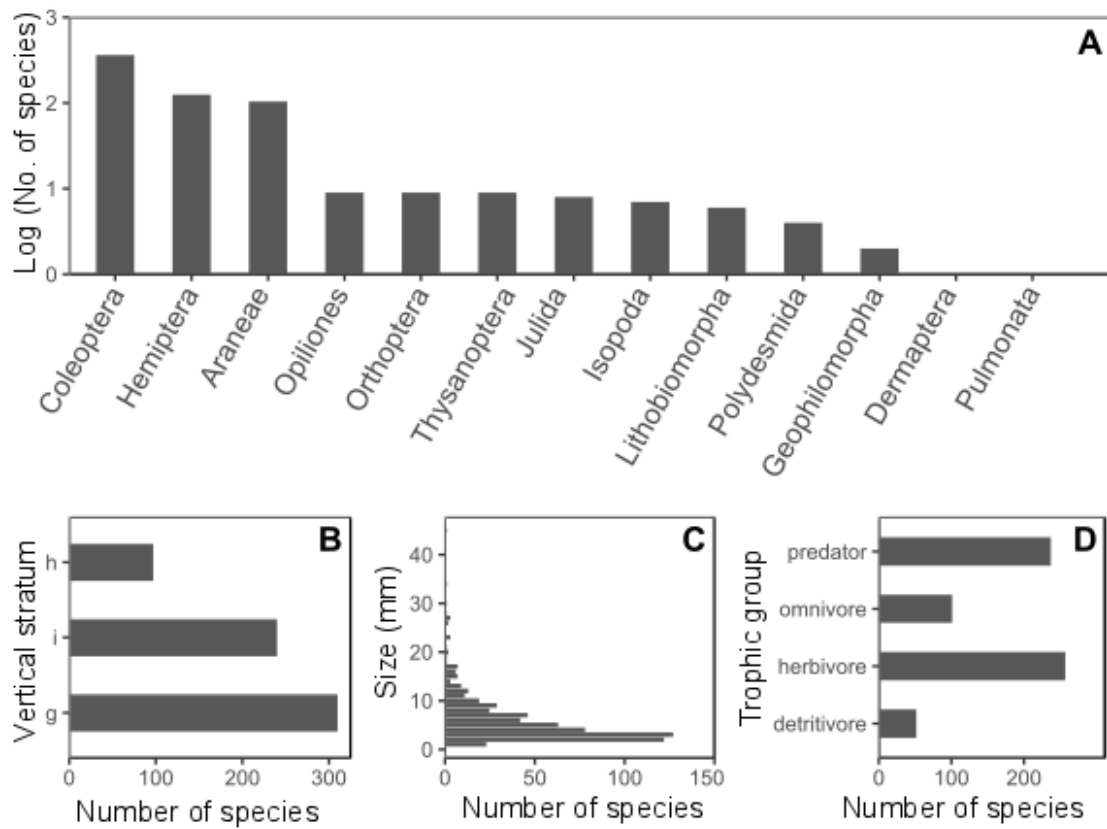


Figure 2. Overview of the number of invertebrate species possessing traits used to establish the Jena Experiment meta-food web. Number of species are shown by A) taxon order B) trophic group, C) vertical stratum of habitat with which they are most commonly associated (g=ground, i=indifferent, h= herb layer), and D) body size class (bin width=1 mm).

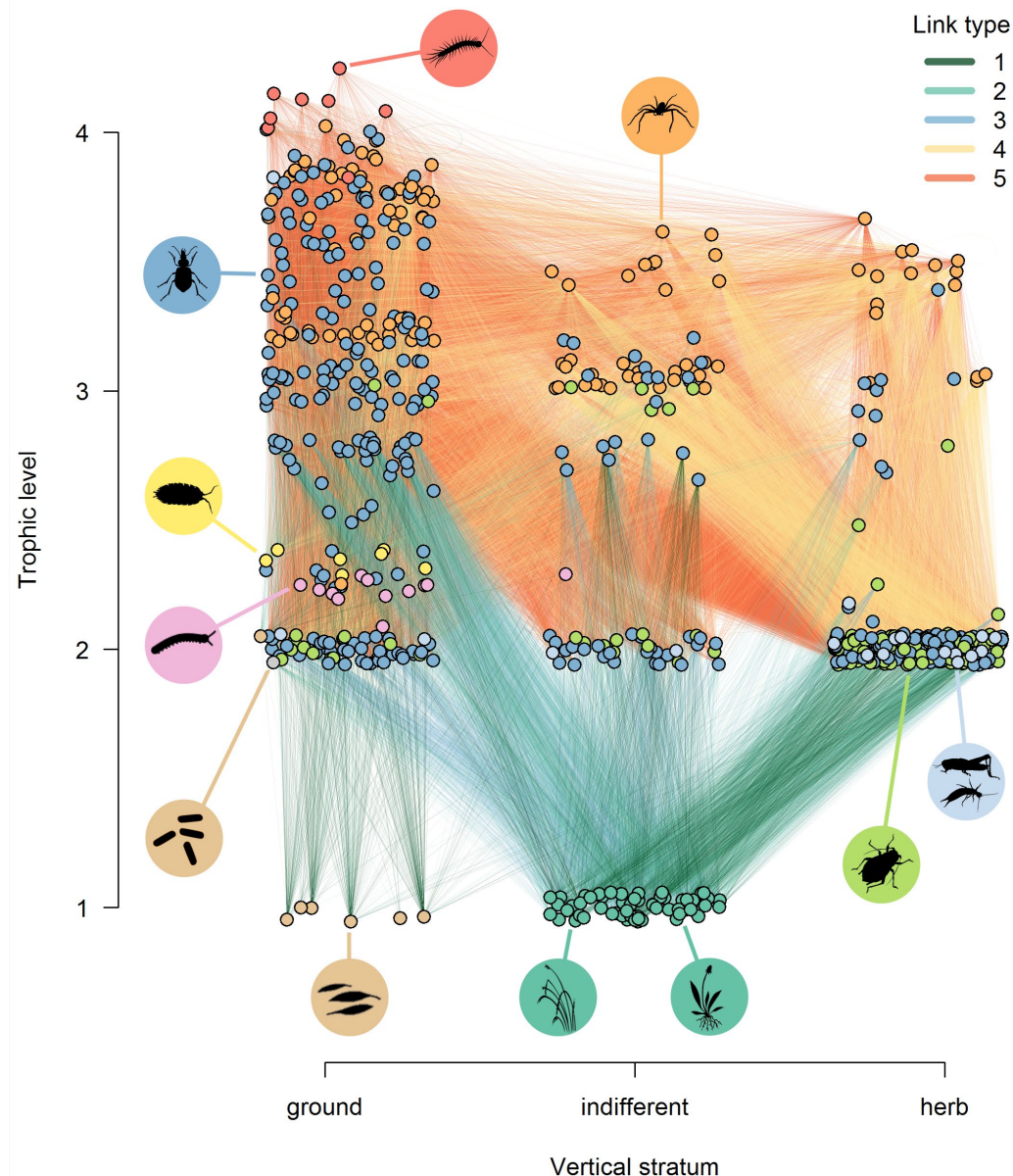


Figure 3. Graphic depiction of the species-level meta-food web of the Jena Experiment.

Each node depicts a species that is positioned one level above the mean trophic level of its resources (Williams and Martinez 2004, Hudson et al. 2013) and the vertical stratum of the habitat with which it is most commonly associated (Rzanny et al. 2013). Both x and y coordinates are jittered for clarity. Species are colored by broad taxonomic classification: plants (dark green), resources and microbes (brown), Gastropoda (grey), Diplopoda (pink), Isopoda (yellow), Insecta (orders Hemiptera [light green], Coleoptera [dark blue] and others [Dermaptera, Orthoptera, and Thysanoptera; light blue]), Arachnida (orange), and Chilopoda (red). Feeding link colors show link types (Table 1).

CLASS V SUPPLEMENTAL DESCRIPTORS

A. Data acquisition methods: The species list was generated from the sampling methods and dates listed in Supplemental Table 1.

Supplemental Table 1. Sampling methods and collection dates used to establish the list of invertebrate species in the Jena Experiment meta-food web.

Year	Sampling method	Date start	Date end
2003	pitfall	13-May-03	27-May-03
2003	pitfall	26-May-03	9-Jun-03
2003	pitfall	2-Jul-03	16-Jul-03
2003	pitfall	23-Jul-03	6-Aug-03
2003	pitfall	14-Aug-03	27-Aug-03
2003	pitfall	29-Sep-03	13-Oct-03
2003	suction	19-May-03	23-May-03
2003	suction	21-Jul-03	25-Jul-03
2003	suction	4-Aug-03	6-Aug-03
2003	suction	25-Aug-03	27-Aug-03
2003	suction	6-Oct-03	10-Oct-03
2005	pitfall	10-May-05	24-May-05
2005	pitfall	26-May-05	9-Jun-05
2005	pitfall	4-Jul-05	18-Jul-05
2005	pitfall	25-Jul-05	8-Aug-05
2005	pitfall	17-Aug-05	31-Aug-05
2005	pitfall	28-Sep-05	12-Oct-05
2005	suction	19-May-05	25-May-05
2005	suction	25-Jul-05	28-Jul-05
2005	suction	16-Aug-05	18-Aug-05
2005	suction	29-Aug-05	31-Aug-05
2005	suction	10-Oct-05	14-Oct-05
2010	pitfall	5-May-10	19-May-10
2010	pitfall	19-May-10	2-Jun-10
2010	pitfall	2-Jun-10	8-Jun-10
2010	pitfall	18-Jun-10	30-Jun-10
2010	pitfall	30-Jun-10	14-Jul-10

2010	pitfall	14-Jul-10	28-Jul-10
2010	pitfall	28-Jul-10	11-Aug-10
2010	pitfall	11-Aug-10	25-Aug-10
2010	pitfall	25-Aug-10	1-Sep-10
2010	pitfall	22-Sep-10	6-Oct-10
2010	suction	7-Jun-10	8-Jun-10
2010	suction	14-Jul-10	19-Jul-10
2012	pitfall	3-May-12	17-May-12
2012	pitfall	17-May-12	31-May-12
2012	pitfall	31-May-12	6-Jun-12
2012	pitfall	20-Jun-12	5-Jul-12
2012	pitfall	5-Jul-12	19-Jul-12
2012	pitfall	19-Jul-12	2-Aug-12
2012	pitfall	2-Aug-12	16-Aug-12
2012	pitfall	16-Aug-12	30-Aug-12
2012	pitfall	13-Sep-12	27-Sep-12
2012	pitfall	27-Sep-12	13-Oct-12
2012	suction	24-Jul-12	24-Jul-12
2012	suction	23-May-12	23-May-12

B. References: References documenting support for feeding links of species in data sets “Jena species traits” and “Jena trophic interactions” are listed in Supplemental Table 2.

Supplemental Table 2. Literature references used to establish feeding interactions (Jena trophic interactions) of the Jena Experiment species pool (Jena species traits). References refer to Microbes¹⁻³, Millipedes^{1,4,5}, Centipedes^{1,6}, Isopoda^{1,7-9}, Dermaptera^{1,10}, Orthoptera^{11,12,13}, Hemiptera¹⁴⁻³², Thysanoptera³³, Coleoptera^{4,8,10,34-96,106-107}, Opiliones⁹⁷⁻⁹⁹, and Araneae⁹⁹⁻¹⁰⁵.

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