The iDiv Ecotron - a flexible research platform for multitrophic biodiversity research

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Abstract

Across the globe, ecological communities are confronted with multiple global environmental change drivers, and they are responding in complex ways ranging from behavioural, physiological, and morphological changes within populations to changes in community composition and food web structure with consequences for ecosystem functioning. A better understanding of global change-induced alterations of multitrophic biodiversity and the ecosystem-level responses in terrestrial ecosystems requires holistic and integrative experimental approaches to manipulate and study complex communities and processes above and below the ground. We argue that mesocosm experiments fill a critical gap in this context, especially when based on ecological theory and coupled with microcosm experiments, field experiments, and observational studies of macroecological patterns. We describe the design and specifications of a novel terrestrial mesocosm facility, the iDiv Ecotron. It was developed to allow the setup and maintenance of complex communities and the manipulation of several abiotic factors in a near-natural way, while simultaneously measuring multiple ecosystem functions. To demonstrate the capabilities of the facility, we provide a case study. This study shows that changes in aboveground multitrophic interactions caused by decreased predator densities can have cascading effects on the composition of belowground communities. The iDiv Ecotrons technical features, which allow for the assembly of an endless spectrum of ecosystem components, create the opportunity for collaboration among researchers with an equally broad spectrum of expertise. In the last part, we outline some of such components that will be implemented in future ecological experiments to be realized in the iDiv Ecotron.

Key words: *food webs, biodiversity and ecosystem functioning, mesocosms, biotic interactions, lysimeters, climate chambers*

Introduction

Ecosystems are threatened by a multitude of environmental change drivers (Pereira et al., 2012, Murphy and Romanuk, 2014, Newbold et al., 2015, Maxwell et al., 2016, Díaz et al., 2019). Over the last few decades, there has been an explosion of studies examining changes in ecological communities and environmental conditions (Hines et al., 2019, Liu et al., 2011, Stork and Astrin, 2014). The desire to draw generalizable conclusions from these studies led to a period of synthesis, during which information from individual studies was compiled allowing for quantitative evaluation of the variation in ecological changes across systems (Gurevitch et al., 1992, Hillebrand et al., 2020, Halpern et al., 2020). Such comprehensive and quantitative synthesis studies enabled researchers to identify generalizable patterns in biodiversity (Calatayud et al., 2020), trends in biodiversity change (Dornelas et al., 2014, Blowes et al., 2019), and relationships between biodiversity and ecosystem functioning (e.g. Cardinale et al., 2012, Gessner et al., 2010, Lefcheck et al., 2015, Soliveres et al., 2016). These high-impact synthesis studies can also serve as a roadmap for designing future experiments, as they help to identify important knowledge gaps which need to be filled in order to better understand the functioning of ecosystems and predict the consequences of climate change.

We have limited empirical evidence for at least three key aspects of environmental changes in ecosystems and communities that draw a roadmap for future research. First, there are limited numbers of ecosystem response variables that have been consistently studied across systems. For example, the most commonly reported response variables are primary production and decomposition (Cardinale et al., 2006, Schmidt et al., 2015a, Schmidt et al., 2015b). However, the few existing multitrophic biodiversity studies indicate that the interactions of higher trophic levels may be particularly important for multiple ecosystem functions (Naeem et al., 1994, Lefcheck et al., 2015, Hines et al., 2015b, Soliveres et al., 2016), and that especially these species might be very vulnerable to environmental changes

80   (Hines et al., 2015a, Voigt et al., 2003). Second, studies tend to investigate limited types of

81   mechanisms and processes underlying changes in biodiversity, ecosystem functioning, and

82   the relationship between the two (Hillebrand et al., 2020). That is, while there is strong

83   emphasis on the effects of global change drivers on changes in species richness (Tilman and

84   Downing, 1994, Harpole et al., 2016, Seabloom et al., 2021, but see Dornales, 2014; Vellend

85   et al., 2013), there is less known about the ecosystem consequences of changes in behaviour

86   (Wilson et al., 2020, Cordero-Rivera, 2017) and community composition (Spaak et al., 2017,

87   Hillebrand et al., 2018) of species that persist in communities. Third, although ecosystems are

88   confronted with complex cocktails of global change drivers (Bowler et al., 2020), so far only a

89   limited number of their types and combinations have been studied in realistic experiments

90   (Rineau et al., 2019, Rillig et al., 2019, but see Schädler et al., 2019, Korell et al., 2020).

91   Especially with regard to climate change, understanding interactions between different

92   environmental variables such as temperature and precipitation, land-use or biodiversity on

93   ecosystem functioning is essential to make predictions for future ecosystem developments

94   and the potential consequences for society (Roy et al., 2017). To address our current

95   knowledge gaps, we need experiments which can simultaneously manipulate and measure

96   different global change drivers (Vanderkelen et al., 2020) and investigate their impacts on a

97   wide range of functional groups and trophic levels of organisms (De Boeck et al., 2020,

98   Komatsu et al., 2019, Korell et al., 2020). Combining such "meta-scale" studies with laboratory

99   and field studies, especially large-scale climate change experiments (like Schädler et al.,

100   2019), provides the opportunity to understand the complex patterns of biodiversity-ecosystem

101   function relationships and their responses to environmental changes as well as the underlying

102   processes that operate across organizational levels of life (cell-individual-population-

103   community-ecosystem; Ferlian et al. (2018)).

104   Here, we introduce the iDiv Ecotron platform (iDiv stands for the German Centre for Integrative

105   Biodiversity Research Halle-Jena-Leipzig in Germany). This platform is a highly flexible

106   experimental infrastructure that was specifically designed to perform multitrophic biodiversity

107   experiments in terrestrial ecosystems (Eisenhauer and Türke, 2018). In the following sections,

108   we describe the iDiv Ecotron specifications and functioning, we highlight a case study

109   experiment as an application possibility, and we provide an outlook on the potential

110   contributions of future ecotron experiments. The concept of the iDiv Ecotron was to create a

111   facility which allows the setup and maintenance of complex communities and manipulation of

112   several abiotic factors in a near-natural way, while simultaneously measuring multiple

113   ecosystem functions. Environmental conditions, such as humidity, nutrient supply, light, and

114   precipitation, can be fully controlled and monitored (for details see App.1), which allows the

115   iDiv Ecotron to be used for the simulation of multiple abiotic scenarios together with scenarios

116   of above-belowground community change. The iDiv Ecotron offers the possibility to study a

117   wide range of ecosystem responses, including above-belowground interactions of plants,

118   microbes, and invertebrates. The platform can accommodate stand-alone experiments, and

119   also provides complementary information to small- and large-scale experiments (lab-ecotron-

120   field). Therefore the iDiv Ecotron links investigations at multiple experimental and spatial

121   scales, and serves as a key component for collaborations between researchers from different

122   disciplines to conduct interdisciplinary studies on the drivers of, and relationship between,

123   biodiversity and ecosystem functioning. Consequently, this platform is likely to provide novel

124   insights into ecosystem responses to global change.

125

Setup & Design of the iDiv Ecotron

Based on some first facilities that were built in England (Imperial College ecotron in Silwood Park; Lawton, 1996) and the USA (Desert Institute Ecocells in Reno, Nevada, Griffin et al., 1996) in the 1990's, highly sophisticated experimental infrastructures, so-called 'ecotrons', started to get established world-wide at the beginning of the 21st century, reflecting the urgent need for such infrastructures accompanied by the rapid evolution in digital technology and electronics (e.g. Ecotron in Montpellier, France, Milcu et al., 2014; ExpoSCREEN in Munich, Germany; Ecotron in Hasselt, Belgium; Biotron in Lincoln, New Zealand). A review with detailed descriptions and comparisons of a variety of ecotrons worldwide can be found in Roy et al. (2020). The idea behind an ecotron is to combine the precision, specificity, and complete control of single independent and response variables of laboratory experiments and the realism and large-scale community- and environment-related aspects of field studies. Roy et al. (2020) define an ecotron as an "…experimental facility comprising a set of replicated enclosures designed to host ecosystems samples, enabling realistic simulation of above- and belowground environmental conditions, while simultaneously and automatically measuring ecosystem processes. Therefore, ecotrons provide continuous information on ecosystem functioning (fluxes of energy and matter)".

The iDiv Ecotron is located in a climate-controlled and blacked out hall on an area of 485 m^2 at the research station of the Helmholtz Centre for Environmental Research - UFZ in Bad Lauchstädt (Saxony-Anhalt, 51° 22' 60N, 11° 50' 60E, 118 m a.s.l.), Germany. The indoor research facility houses 24 identical experimental units (hereafter EcoUnits, see Fig. 1), each of which can contain one to four ecosystems, separated above- or belowground, or both. In this way, up to 96 sub-units with various biotic and abiotic variables to be manipulated and measured independently can be set up. These features are new in the world of ecotrons: the iDiv Ecotron, as an indoor facility, is completely independent of external weather conditions (unlike, for example, the Hasselt Ecotron in Belgium) and at the same time provides a large

number of individual independent chambers (unlike other indoor facilities, such as ExpoSCREEN in Munich, Germany, or the Montpellier Ecotron mesocosms in France; see Roy et al. 2020). The iDiv Ecotron concept was developed in cooperation with numerous scientists and technicians from iDiv, including strong participation by the UFZ, national and international collaborators, and the companies 'EMC - Gesellschaft zur Erfassung und Bewertung von Umweltdaten mbH', and 'Umwelt-Geräte-Technik GmbH (UGT), Müncheberg'.

EcoUnits are experimental chambers with the outer dimensions of 1.55 m × 1.55 m × 3.20 m (L × W × H), comprising a lower part, which can be filled with soil (belowground part), an upper part (aboveground part), and a technical section on the top. The frame of the chamber is constructed of aluminum construction profiles providing stability and flexibility.

The belowground part contains a container with internal dimensions of 1.24 m × 1.24 m × 0.80 m (L × W × H) made of welded PE-HD and a steel bottom. It can be filled with up to 1.23 m^3 of soil, or alternatively equipped with four steel cylinders (lysimeters) measuring 0.50 m × 0.80 m (D × H), each of which can hold 0.16 m^3 of soil. The container as well as the lysimeters feature pluggable openings in three different depths (9.5 cm, 21.5 cm, and 43.5 cm), where sensors for soil temperature, soil moisture, and water potential can be inserted. Additional larger openings in the same depths as those for the sensors offer the opportunity to install minirhizotrons (acrylic glass tubes) for horizontal monitoring of root development using a portable root scanner (see Möller et al., 2019).

Besides manually filling the lysimeters with soil, they can be used to excavate intact soil monoliths, including aboveground vegetation, directly from the field. This enables precise investigations of almost undisturbed soil systems, preserving their structure and stratification as well as their faunal and microbial soil communities. Both the lysimeters and the containers provide a living space of sufficient size to establish and study belowground organisms and processes. To achieve a near-natural soil temperature gradient with temperature decreasing from the surface to deeper soil depths, the bottom of the soil container was fitted with a coil

178   that circulates a cooling medium. This system can be regulated individually for each EcoUnit

179   and automated with the data from the above- and belowground temperature sensors.

180   To allow pore water sampling and near natural drainage of water from the soil system, four

181   suction systems are installed at the bottom of the soil container or one in each lysimeter. Each

182   suction system consists of a suction cup ring with 8 suction cups, a pump, a control module,

183   and two glass bottles. By applying negative pressure (max. -60 kPa), the suction systems

184   continuously extract and collect pore water. When one bottle is filled, the control unit of each

185   suction system automatically switches to the alternate bottle and empties the first one. To

186   quantify the volume of water sampled, the system counts the number of bottle changes. This

187   enables a continuous supply of soil water for chemical analyses and an automated recording

188   of the total amount of collected water. Simultaneously, the negative pressure applied at the

189   bottom of the lysimeter lowers the water potential from there up and reduces "unnatural" high

190   plant transpiration. When the soil column is cut over the course of the monolith extraction, the

191   water potential at the cut level becomes zero - it is brought to atmospheric pressure, which

192   eases and therefore increases the extraction of water by plants. Here, the suction system can

193   be used to apply the pressure that corresponds to the natural in situ water potential at that

194   depth. This allows for these ecosystems to further approximate natural conditions (Groh et al.

195   2016). Optionally, single suction cups can also be installed in three different depths (9.5 cm,

196   21.5 cm, and 43.5 cm) by using the pluggable openings.

197   The aboveground part, with internal dimensions of 1.46 m × 1.46 m × 1.50 m (L × W × H),

198   provides sufficient space for communities of large herbs or tree saplings (see Fig. 2) including

199   their complex multitrophic interaction networks. In each quarter, a video camera can be

200   installed (for details on the camera system see App.1), e.g. for monitoring vegetation

201   development over time (Ulrich et al., 2020) or insect behavior, such as movement patterns,

202   flower visitation of pollinators, and habitat use. By using infrared lights, the cameras can also

203   operate in darkness.

204 The aboveground part is further equipped with an irrigation system consisting of a flow meter

205 and four electromagnetic valves with fixed nozzles. By sequentially processing the opening

206 times of the valves, each quarter of an EcoUnit can be automatically provided with individual

207 volumes of water at programmable times. All irrigation systems are supplied with deionized

208 water from a central reverse osmosis system. To compensate for the flow resistance caused

209 by different lengths of supply hoses to each EcoUnit, the water pressure at the water treatment

210 plant is increased to approx. 4 bar (400 kPa) and then reduced to a constant level of about 2

211 bar (200 kPa).

212 Ambient air temperature is maintained centrally in the Ecotron hall, but the air flow rate of each

213 sub-unit can be regulated individually. Climatic conditions are recorded by combined humidity

214 and temperature sensors installed in each quarter of an EcoUnit, usually placed at a height of

215 40 cm above soil surface. Conditions are continuously compared with those of the hall and,

216 as needed, automatically adjusted by increasing or decreasing the fan speed of the ventilation

217 system. All four quarters of the EcoUnit can be regulated individually.

218 Further, the top part of the EcoUnits is equipped with a diffuser holding 4 LED lamps adjustable

219 in color and intensity. The light system provides three individually dimmable color channels

220 (400 nm - 405 nm, 460 nm - 475 nm, 625 nm - 720 nm) as well as a dimmable white channel

221 (5000 K + 3000 K), and a binary (ON/OFF) infrared channel (840 nm - 850 nm). For the overall

222 luminance as well as for each color channel, the intensity can be set from 0% to 100%

223 individually, determining the general light color. This can be done either manually or

224 automated in an hourly resolution with an automatically linear transition between the settings.

225 In this way, the relative proportion of different wavelengths within the light spectrum can be

226 modified (e.g. a higher proportion of red light at dawn and dusk). The maximum photosynthetic

227 active radiation (PAR) 5 cm above the standard soil surface can reach about 400 μmol s^{-1} m^{-2}

228 on average (detailed information on the heterogeneity of illumination can be found in App.2).

229 Two electrical cabinets provide the power supply for the lamps and a local control unit for all

230 sensors and actuators.

231 Control commands and settings of all manipulable environmental parameters are stored in a

232 central database and get transmitted to each EcoUnit via a network. In turn, the execution

233 confirmations as well as the timestamped sensor data of each EcoUnit are logged in the same

234 database. This asynchronous communication between EcoUnits and database server

235 provides a high operational reliability and independence of network's capacity bottlenecks. A

236 simple graphical user interface eases the handling of database entries.

237

Case Study - *Effects of aboveground predators on aboveground-belowground interactions and ecosystem functions*

Rationale

Aboveground-belowground interactions are known to determine the functioning of terrestrial ecosystems (Scheu, 2001, Wardle et al., 2004). Previous work has shown that aboveground invertebrate predators can induce trophic cascades that "trickle-down" to affect soil food webs and a broad range of ecosystem functions (Wardle et al., 2005). Here we present a case study conducted in the iDiv Ecotron to test how plant community composition may affect such trickle-down effects. Further, as plant-mediated effects of aboveground predators may additionally depend on the activity of soil ecosystem engineers, which structure the environment for (Brown, 1995, Eisenhauer, 2010) and the resource supply of soil food webs (Eisenhauer, 2010, Schwarzmuller et al., 2015), we investigated the effects of soil fauna on multitrophic diversity and ecosystem functions. The unique functionality of the iDiv Ecotron enabled us to study potential cascading effects of aboveground predators on herbivores, plants, and soil food webs, and how these effects are modulated by decomposer communities in the soil. Specifically we tested (1) if the target plant biomass would be lower in the presence of herbivores, an effect that would be alleviated by the presence and higher density of predators (e.g. Wardle et al., 2005). We further hypothesized (2) that the identity of the neighboring plant community will affect the biomass of the target plant with biomass being higher in a community with herb species compared to grass species due to elevated competition for soil resources in the presence of grasses (Eisenhauer and Scheu, 2008). Moreover, we expected (3) the presence of decomposers (earthworms and Collembola) to affect the tritrophic interactions aboveground, as decomposition and mineralization processes in soil can significantly alter the performance of the target plant (Scheu, 2003, van Groenigen et al., 2014) as well as the competition with the surrounding vegetation (Eisenhauer and Scheu, 2008, Sabais et al.,

263 2012). Finally, we hypothesized (4) that there will be trickle-down effects of aboveground

264 predators on soil nematode density and species richness due to altered resource supply and

265 that soil food web responses to these trickle-down effects will be modulated by earthworm

266 presence as they significantly change the structure of the environment for and resource supply

267 of other soil organisms (Brown, 1995, Eisenhauer, 2010).

268

Methods

270 In six EcoUnits in a lysimeter configuration a tritrophic system got established comprising a

271 target plant (*Vicia faba* L.), its host-specific aphid (*Acyrthosiphon pisum* Harris), and a predator

272 exclusively feeding on aphids (*Coccinella septempunctata* Linnaeus; details on initial densities

273 can be found in (App. A.1). We further included a soil fauna treatment (with and without soil

274 fauna) to test, if predator effects are modulated by the presence of macro- and meso-

275 decomposers in the soil; and a "plant neighbor" treatment to test plant responses in different

276 competitive environments and to increase variation for reproducibility purposes (Milcu et al.,

277 2018). Concisely, we established an experimental setup with three treatment factors

278 comprising *aboveground invertebrates*, *belowground invertebrates* and *surrounding*

279 *vegetation* (see Fig. 3). Each treatment combination was replicated three times. While soil

280 compartments were all fully isolated one from another (four per EcoUnit), the aboveground

281 compartments allowed for an exchange of invertebrates between lysimeter pairs with an

282 acrylic glass barrier of 15 cm height preventing the migration of soil invertebrates between

283 lysimeters. In this way, there were two independent experimental units in each of the six

284 EcoUnits resulting in twelve independent units and 24 sub-units in total (more details on the

285 experimental setup and environmental conditions can be found in App. A.2).

286

287

288   Details on treatment factors:

289   (1) *aboveground invertebrates*; the treatment was established to test if predator effects depend

290   on their density (**4** *levels:* all aboveground invertebrates absent *[Control]*, only aboveground

291   herbivores present *[Herbivores only]*, aboveground herbivores present with aboveground

292   predators in low density *[Coccinella low]*, aboveground herbivores present with aboveground

293   predators in high density *[Coccinella high]*).

294   (2) *belowground invertebrates*; to half of the lysimeters earthworms and Collembola were

295   added to test if predator performance is modulated by the presence of macro- and meso-

296   decomposers in the soil (**2** *levels:* earthworms and Collembola present *[with soil fauna]* versus

297   earthworms and Collembola absent *[no soil fauna]*); soil invertebrate species list and initial

298   densities can be found in App. A.3).

299   (3) *surrounding vegetation*; the focal plants (*Vicia faba* L) were each surrounded by a herb or

300   grass monoculture (**4** *levels: Bellis perennis* L.*, Centaurea jacea* L., *Festuca pratensis* Huds.*,

301   *Holcus lanatus* L.; details on plants can be found in App. A.4).

302   Analyzed response variables were dry weight (g) of the focal plant (*Vicia faba*), nematode

303   density, nematode species richness (all three recorded during the harvest at the end of the

304   experiment), maximum numbers of aphids (peak number of individuals counted in one

305   assessment during the experiment), days of aphid infestation (number of days beans were

306   infested with aphids; details can be found in App. A.5). The experiment ran for 124 days, from

307   03 February 2017 to 06 June 2017.

308

309   <u>Results</u>

310   The target plant (for brevity 'bean' in the following) dry weight differed significantly depending

311   on the neighboring plant species ($F_{3, 48} = 5.16$, $P < 0.01$; Fig. 4, App.8) and the aboveground

312 invertebrate treatments ($F_{3, 48}$ = 6.48, P < 0.001; Fig. 4, App.8), whereas it did not differ among

313 belowground invertebrate treatments as well as with any of the two- or three-way interactions

314 of the three variables tested. Bean dry weight was lowest in patches with *B. perennis* and *H.*

315 *lanatus*, whereas it was significantly higher in *C. jacea* patches (Fig. 4). Furthermore, bean

316 dry weight was highest in the aboveground invertebrate *'Control'* and the *'Coccinella high'*

317 treatments, whereas it was lowest in the *'Herbivores only'* treatment.

318 The maximum number of aphids and number of days of aphid infestation differed significantly

319 between the aboveground invertebrate treatments ($F_{1, 24}$ = 8.24, P = 0.01; Fig. 4, App.8; and

320 $F_{3, 48}$ = 63.19, P < 0.001, respectively; App.8). Further, the maximum number of aphids showed

321 significant differences in the interaction between plant neighbor species and belowground

322 invertebrates ($F_{3, 24}$ = 5.82, P = < 0.01; Fig. 4, App.8). In general, numbers of aphids were

323 higher in the *'Coccinella low'* treatment compared to the *'Coccinella high'* treatment.

324 Depending on the plant neighbor identity, maximum number of aphids slightly decreased (*B.*

325 *perennis* and *F. pratensis*) or increased (*C. jacea* and *H. lanatus*) with the presence of

326 belowground invertebrates, but effects were not statistically significant.

327 Nematode densities differed significantly only between plant neighbor species ($F_{3, 48}$ = 2.86, P

328 = 0.05; App.8). Highest numbers were found in patches where *C. jacea* was planted and

329 lowest numbers in plots with *F. pratensis* (significant differences were found only between

330 these two). For nematode species richness, only the interaction between plant neighbor

331 species and the aboveground invertebrate treatment was significant ($F_{9, 48}$ = 2.21, P = 0.04;

332 Fig. 4, App.8). Although the post-hoc Tukey's HSD test showed no significant differences

333 between factor levels, nematode species richness was lowest in the *'Herbivores only'*

334 treatment in the presence of *F. pratensis*, while it was highest in the 'Control' treatment in the

335 presence of *C. jacea*.

Discussion

In contrast to our expectations, beans did not generally benefit from growing in herb communities, while being suppressed by more dominant nitrophilous grasses (Eisenhauer and Scheu, 2008). We observed opposing effects for the two grass species and for the two herb species on bean biomass. Among the four neighboring plant species, *H. lanatus* produced by far the highest amount of aboveground plant biomass (139.5 g) at the end of the experiment compared to the other three species (*F. pratensis*: 92.1 g, *C. jacea*: 51.1 g, *B. perennis*: 5.3 g), and, as graminoid species typically produce a dense and large root system, we speculate that also root biomass was highest (not assessed in this study). Thus, both enhanced aboveground light competition and belowground competition for resources may have contributed to an overall advantage in resource acquisition over the bean, causing low bean biomass. Indeed, it has been often confirmed that grasses are stronger competitors compared to herbaceous species (Tilman, 1982, Del-Val and Crawley, 2005). Moreover, another potential explanation for the patterns found in our study may be that in patches of low biomass, e.g., in *B. perennis* patches, the habitat structure for predators was comparably low leading to a migration to more favorable habitat structures. This effect may have cascaded to lower trophic levels increasing abundances of herbivores and decreasing plant performance (Romero and Koricheva, 2011). The importance of such non-trophic interactions based on habitat structure has been often highlighted (Kalinkat et al., 2013, Majdi et al., 2014).

Our results confirm the often found tritrophic relationships between predators, herbivores, and primary producers, where predators, in our case ladybirds, exert a top-down control on aphid abundances which, in turn, have a top-down effect on the bean (Romero and Koricheva, 2011). Surprisingly, the effects of plant neighbor species on aphid abundances were opposing for communities without and with belowground invertebrates. These findings highlight the significance of aboveground-belowground interactions and show that decomposers can influence aboveground multitrophic interactions by altering the competition between plants

362 (Wardle et al., 2004). Moreover, we found that trickle-down effects of aboveground

363 invertebrates on soil food webs (here represented by soil nematode species richness) depend

364 on plant community composition. This finding suggests that the competitive environment of a

365 focal plant can alter its effects on soil community composition, potentially through changes in

366 the amount and quality of plant-derived resources entering the soil (Hooper et al., 2000).

367 Taken together, our study shows distinct interaction effects between aboveground and

368 belowground invertebrate communities on multitrophic interactions and community

369 composition in the sub-compartments. These changes are likely to alter how communities

370 function, which may have subsequent feedback effects on nutrient cycling and community

371 composition. The results of our study highlight the need for infrastructures that allow to

372 manipulate food webs of high complexity, which can hardly be realized experimentally under

373 field or simplified laboratory conditions, and at the same time, taking advantage of measuring

374 and controlling a large fraction of other non-targeted parameters including environmental

375 conditions.

376

Outlook

Over the last several decades ecologists have written thousands of papers about changes in climate and biological communities. Yet, some important knowledge gaps remain. Here we discuss the relevance of mesocosm research as an underappreciated scale of inquiry. We further develop this line of reasoning by describing three opportunities where the iDiv Ecotron is particularly well suited to address challenges limiting an integrative understanding of biodiversity and ecosystem functioning.

Mesoecology is an important and often overlooked scale in environmental change research (Stewart et al., 2013). While macroecological studies provide more realistic abiotic and biotic context for investigating ecosystem processes, complex communities and environmental conditions can only be controlled, and causality of patterns inferred, to a very limited extent, and often with very few replicates (Lawton et al., 1993, Eisenhauer and Türke, 2018). On the other hand, laboratory microcosm studies can fully control and alter external factors and allow for high replication (Benton et al., 2007). However, laboratory studies are often limited to investigating single mechanisms and processes under artificial and simplified environmental conditions (Lawton et al., 1993). They are prone to experimental artefacts caused by the simplification of complex interactions which may bias results and induce misleading conclusions (Roy et al., 2020, Milcu et al., 2018, Carpenter, 1996, Carpenter, 1999, Schindler, 1998). The iDiv Ecotron provides an important middle ground, especially with the possibility of extracting and implementing up to 96 intact soil monoliths which allows for precise investigations of almost undisturbed soil systems, while preserving their structure and stratification as well as their faunal and microbial soil communities. Mesocosm experiments close the gap between small- and large-scale studies and they allow scientists working together across levels of organization from cells to ecosystems to test basic and applied ecological questions. However, attempts to do so will profit from including a few key aspects of research that serve as future opportunities.

Opportunity 1: Multi-trophic diversity change

Although many studies have evaluated responses of plant species to environmental variation, ecologists have yet to demonstrate the collective importance of these responses for the full complement of plants' interaction partners above and below the ground. This is particularly important because not all taxa that interact with plants perceive environmental variation at the same scale (Veen et al., 2019, Heinen et al., 2018). Therefore, although it has been shown that diversity can beget diversity, and patterns in plant diversity can parallel patterns of soil diversity and aboveground consumer diversity (Scherber et al., 2010, Eisenhauer et al., 2013), these patterns may be mismatched (Cameron et al., 2019) and/or further decoupled by environmental change drivers (Bardgett and Wardle, 2010, Thakur, 2020). Future iDiv Ecotron experiments will evaluate differences in spatial and temporal response to drivers that may explain mismatches in above- and belowground biodiversity (Eisenhauer and Türke, 2018). The iDiv Ecotron allows for simultaneous manipulation of aboveground and belowground biodiversity, with particular emphasis on belowground sub-systems through the use of intact soil cores, the examination of roots via rhizotrons, and large enough spatial scale to examine differences in patterns of aboveground and belowground diversity. Rigorously testing factors that influence aboveground-belowground relationships is critical, because they form key pathways by which environmental variation influences community assembly, biodiversity effects on ecosystem functioning, and the impacts of environmental change on community dynamics. To develop effective plans to conserve biodiversity, we need meso-scale empirical studies that test the mechanisms underlying effects of environmental drivers on aboveground-belowground biodiversity and ecosystem functioning.

Opportunity 2: Beyond presence/absence—Behavioural and chemical mechanisms of plants and animal interactions

Traditionally, experimental examinations of food web interactions have been conducted by stocking simplified communities into microcosms or field plots and quantifying the outcome of

429   the interactions by counting the presence and abundance of species after a designated time
430   period. It is likely that phenotypic changes (e.g. changes in behaviour, chemistry, or
431   morphology) serve as precursors to the numerical changes in community composition that are
432   typically quantified, or that phenotypic changes can drive major changes in ecosystem
433   functioning on their own (Matthews et al., 2011, Turcotte and Levine, 2016). Yet, phenotypic
434   responses are more often evaluated in highly simplified communities with limited emphasis on
435   interaction complexity. We see considerable potential for iDiv Ecotron studies to extend highly
436   simplified laboratory experiments showing effects of environmental drivers on phenotypic
437   responses (e.g. behavioural, morphological, and physiological change). Changes in local
438   foraging and behaviour/activity patterns may be an important mechanism underlying changes
439   in biodiversity-ecosystem function relationships (Jeltsch et al., 2013). The iDiv Ecotron can be
440   fit with a landscape of sensors for detecting movement of animals tagged with RFID chips.
441   Repulsed (or aggregated) animal activity patterns can point to the importance of non-trophic
442   and trait mediated interactions (e.g. fear). Such behavioural changes are not limited to
443   animals. For example, behaviour changes of plants emission of plant volatiles can be turned
444   off and on depending on plants interaction partners. Plant volatiles play key roles in plant
445   defence against aboveground and belowground herbivores, plant competition, and plant
446   communication (Pierik et al., 2014). Yet, research of plant volatiles is often conducted on
447   isolated plants or pairs of plants. These aspects of phenotypic changes (animal movement,
448   plant volatiles) are difficult to assess in field conditions where signals may be detected by
449   ecological communities but not my scientific instruments due to difficulties relocating animals
450   in larger more complex landscapes, or buffering effects of wind. Future iDiv Ecotron
451   experiments will examine the role of aboveground-belowground plant and animal behaviour in
452   complex communities.

453   *Opportunity 3: Multiple drivers of environmental heterogeneity and environmental change*

454   We have only begun to identify the full array of environmental changes confronting
455   ecosystems today (Bowler et al., 2020). The iDiv Ecotron allows for independent manipulation

456   of several abiotic factors (e. g. precipitation, light, nutrients, and temperature) in gradient-

457   based or factorial combinations. Non-additive, synergistic or unexpected responses may be

458   detected from heretofore untested combinations of environmental change drivers. There is

459   also much potential to use the iDiv Ecotron to examine the influence of minor or extreme levels

460   of drivers and to detect non-linear relationships between drivers and ecosystem responses

461   (Damgaard et al., 2018, De Boeck et al., 2015). Therefore, the iDiv Ecotron is an ideal tool to

462   complement environmental change experiments where ecological responses are evaluated

463   over longer time periods or greater spatial scales, but at the cost of examining a reduced

464   number of scenarios (e.g. Schädler et al., 2019). Future studies may therefore be considered

465   as a step towards precision and mechanistic understanding supplementing other laboratory

466   or field studies.

467   In conclusion, the iDiv Ecotron provides a flexible collaborative research platform that operates

468   at an intermediate scale, connecting simplistic microcosm experiments and real-world

469   heterogeneity. Their size allows for evaluation of naturally complex aboveground-belowground

470   interactions, often overlooked mechanisms (e.g. behaviour, plant volatiles), as well as a broad

471   range of environmental drivers. Therefore, this robust experimental facility can help to fill

472   several critical knowledge gaps identified in synthesis studies. The iDiv Ecotron will be used

473   to assemble, disassemble, and reassemble ecological communities in rigorous tests of basic

474   and applied ecological questions. We start with an empty box with strong technical capabilities

475   to control environmental conditions, endless possible combinations of species, and an open

476   call to potential collaborators: What would you do if you could rebuild the world?

477

Additional Information

App.1

Table App.1

App.2

Figure App.2

App.3 - Aboveground invertebrates

To test for effects of aboveground invertebrates on tritrophic interactions and nematode communities, we implemented different combinations of herbivore and predator species presence and absence. We used the pea aphid *Acyrthosiphon pisum* Harris as aboveground herbivore feeding specifically on the broad bean *Vicia faba* L. Eight mature individuals were added to each replicate of respective treatments between April 27th and May 3rd. We used adult beetles of the seven-spot ladybird (*Coccinella septempunctata* Linnaeus) as specialized aphid predators which were added in two different densities (two or four individuals) on May 10th to respective treatments. In total, we tested four aboveground treatments: Control (no invertebrates), Herbivores only (with aphids, without ladybirds), Coccinella low (with aphids, with two individuals of *C. septempunctata*), and Coccinella high (with aphids, with four individuals of *C. septempunctata).*

App.4 - Experimental setup

The 24 Lysimeters were filled with steam-sterilized top soil (purchased at Bauzentrum Farys GmbH, Laucha). For sterilization, the soil was subjected to water steam at approx. 100°C for 30 minutes. Such sterilization leads to a heavy release of nutrients due to the death of soil organisms (Alphei and Scheu, 1993, Trevors, 1996), which is why the soil was thoroughly rinsed with tap water afterwards (Jager et al., 1970). The soil was inoculated with nematode and microbial communities on February 2nd 2017, marking the start of the experiment. Live soil organisms were extracted from top soil of an experimental grassland site (Jena Experiment, Roscher et al., 2004). We added four independent samples of soil wash solution (extracted from 100 g of soil each, filtered through a 125 μm sieve) to each lysimeter on February 3rd. In addition, we added three independent inoculates of nematode solution between February 2nd and March 10th, which were previously live-extracted from 20 g wet soil each, following the modified Baermann funnel method (Cesarz et al., 2019; for details on nematode communities in the Jena Experiment, see Eisenhauer, Migunova, Ackermann, Ruess, & Scheu, 2011 and Cesarz et al., 2017). To exclude that unintended additions of nematodes might have confounded the controlled inoculation, soil samples from the sterilized soil filled into lysimeters were extracted with the same method and yielded no live nematodes. The following environmental parameters were set in the EcoUnits: light/dark cycle 16/8 h (max illumination at day, gradual change), temperature 21°C at day and 17°C at night (gradual change over the course of 3 h), irrigation of 400 ml on each lysimeter area daily at 4 am, soil temperature set to 17°C in 43.5 cm soil depth.

App.5 - Soil invertebrates

The steam-sterilized soil (Dietrich et al., 2020) got inoculated with microorganisms and nematodes (see App.4). To test for interactions between the aboveground tritrophic system

523 and belowground invertebrate presence (meso-/macro-fauna), we added the following soil

524 invertebrates to one of the two lysimeters in each replicate: 15 juvenile anecic earthworms

525 (*Lumbricus terrestris* Linnaeus, mean weight 4.4 g) and 20 individuals each of two Collembola

526 species (*Folsomia candida* Willem, *Protaphorura armata* Tullberg). Collembola populations

527 have been shown to develop rapidly in the experimental soil until the carrying capacity of the

528 system is reached (Eisenhauer et al., 2011). Fifty g of commercial grassland litter was

529 provided as substrate to both lysimeters (bunny® Frischgras-Heu). Since hay is a natural

530 product, its grain properties vary according to season. Typically, the in Table App.5 shown

531 groups of plants are included.

532 **Table App.5**

533

534

535 App.6 - Plants

536 Nineteen 23-day old seedlings each of two herbaceous *(Bellis perennis L., Centaurea jacea*

537 *L.)* and two grass species *(Festuca pratensis Huds., Holcus lanatus* L.) were transplanted in

538 regular distances of 5 cm and within monoculture quarters (see App.6) into each lysimeter on

539 February 16th to mimic a simplified grassland community. In the center of each monoculture

540 quarter, a single individual of an 8-day old broad bean seedling (*Vicia faba* L., variety "Dreifach

541 Weiße", Bruno Nebelung GmbH) was transplanted on April 19th, representing the specific host

542 plant of aboveground herbivores. Consequently, there were four host plant individuals per

543 lysimeter and thus eight individuals per replicate.

544

545 App.7 - Measurements

546 Numbers of aphids on each bean were counted every 7 days. For analyses, we used the peak

547 number of all assessments during the experiment (hereafter called 'maximum number of

548   aphids'). Furthermore, we recorded the number of days beans were infested with aphids by

549   counting live aphids on each bean individual from first discovery until last discovery; last

550   discovery could either be the end of the experiment or the time a bean got in a bad status and

551   was not a suitable host for aphids anymore.

552   All beans were harvested 49 days after their transplantation by taking 5-cm-diameter soil cores

553   to a depth of 10 cm with beans in their center. The soil was sieved through a 2-mm sieve,

554   bean roots were extracted and both were stored at 4°C until further processing. After the

555   removal of aphids the bean aboveground parts were dried at 45°C for 3 days and weighed.

556   Nematodes were extracted from the previous stored soil following a modified Baermann

557   technique with an extraction time of 48 h (Cesarz et al., 2019). Extracted nematodes were

558   transferred to formalin (4%) and counted to obtain the total density of nematodes.

559   Subsequently, 100 individuals were randomly selected and identified to genus level following

560   (Bongers and Bongers, 1998) or separated into morphospecies where not possible.

561

562   App.8 - GLMM

563   **Table App.8**

564

565

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Tables

Table App.1: Abiotic parameters of an EcoUnit, control and data storage options; combined temperature/humidity sensors: *MELA FE09, Galltec Meß- und Regeltechnik GmbH Bondorf, Germany*; integrated flow meter: *FCH-midi-POM 97478976, B.I.O.-TECH e.K. Vilshofen, Germany*; temperature/moisture sensors belowground: *SMT100, TRUEBNER GmbH Neustadt, Germany*; observation cameras: *YUC-Hi82M, Yudor Technology Co, Ltd Tao Yuan City 324, Taiwan*.

Parameter	Controlling	User interface	Sensing
air temperature	via adjustable ambient temperature of hall	GUI	4 combined temperature/humidity sensors
air humidity	indirect only by air temperature and air flow rate	-	4 combined temperature/humidity sensors
air flow rate	by blower speed	GUI	manually by air velocimeter
lighting timing	1 h setting resolution with automatically calculated intermediate dim steps for each channel	GUI	logging of execution confirmation only
light intensity	nominal 1% setting resolution with internal mapping to nearest dim step	GUI	logging of execution confirmation only
light color mix	4 dim channels (UV, blue, red, NIR); 1 non dim channel (FIR)	GUI	logging of execution confirmation only
irrigation volume	50 ml setting resolution	GUI	integrated flow meter
irrigation timing	1 h setting resolution	GUI	logging of execution confirmation only

soil temperature	by cooling at the bottom down to ~10 °C with resulting temperature gradient to soil surface	GUI	up to 12 combined temperature/moisture sensors in three levels belowground
soil moisture	indirect only by change of irrigation volume, soil water removal, and the manipulation of evaporation rate by air flow rate	-	up to 12 combined temperature/moisture sensors in three levels belowground
suction low pressure	1 kPa setting resolution with low pressure down to -60 kPa below ambient air pressure	GUI	each suction system includes an integrated pressure sensor
video observation	orientation of vision and operation mode manually only	camera's web GUI	observation camera
still pictures	by external script with access to video stream of running cams	camera's web GUI + Linux shell	observation camera

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965 **Table App.5** Species list of the commercial grassland litter from bunny® Frischgras-Heu
966 provided as substrate to both lysimeters.

English name	Latin name
Timothy (grass)	*Phleum pratense*
Meadow fescue	*Festuca pratensis*
Meadow foxtail	*Alopecurus pratensis*
Ryegrass	*Lolium sp.*
Red fescue	*Festuca rubra* agg.
Kentucky bluegrass	*Poa pratensis*
Bent grass	*Agrostis sp.*
Cat grass	*Dactylis glomerata*
Common dandelion	*Taraxacum officinale*
Common silverweed	*Potentilla anserina*
Mouse-ear chickweed	*Cerastium sp.*
Yarrows	*Achillea sp.*
Ribwort plantain	*Plantago lanceolata*
White clover	*Trifolium repens*
Red clover	*Trifolium pratense*
Common bird's-foot trefoil	*Lotus corniculatus*

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969　**Table App.8** Effects of aboveground (AG) and belowground (BG) invertebrates and bean plant neighbor species identity as well as their interactions on five response variables using GLMM type III sum of squares
970　analyses; significant effects (P < 0.05) are indicated in bold font; *sp. richness*: species richness, *max. no. of aphids*: maximum number of aphids.

| | Response variable | | | | | | | | | | | | | | |
| Grouping variable | Bean dry weight | | | Nematode density | | | Nematode sp. richness | | | Max. no. of aphids | | | Days aphid infestation | | |
	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
AG invertebrates	**3, 48**	**6.48**	**< 0.001**	3, 48	0.16	0.92	3, 48	0.51	0.67	**1, 24**	**8.24**	**0.01**	**3, 48**	**63.19**	**< 0.001**
BG invertebrates	1, 48	0.26	0.61	1, 48	1.01	0.32	1, 48	1.99	0.16	1, 24	0.22	0.64	1, 48	0.20	0.65
AG invertebrates*BG invertebrates	3, 48	1.37	0.26	3, 48	0.84	0.48	3, 48	0.12	0.95	1, 24	0.25	0.62	3, 48	1.25	0.30
Neighbor species	**3, 48**	**5.16**	**< 0.01**	**3, 48**	**2.86**	**0.05**	3, 48	1.62	0.20	3, 24	1.42	0.26	3, 48	0.36	0.78
Neighbor species*AG invertebrates	9, 48	0.22	0.99	9, 48	1.40	0.22	**9, 48**	**2.21**	**0.04**	3, 24	0.44	0.73	9, 48	0.87	0.56
Neighbor species*BG invertebrates	3, 48	0.30	0.82	3, 48	1.25	0.30	3, 48	0.62	0.61	**3, 24**	**5.82**	**< 0.01**	3, 48	1.58	0.21
Neighbor species*AG invertebrates*BG invertebrates	9, 48	0.92	0.52	9, 48	0.76	0.65	9, 48	0.86	0.56	3, 24	0.24	0.87	9, 48	0.30	0.97

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Figure captions

Figure 1 Illustration of an EcoUnit; (A) construction drawing with corner cutout to visualize the technical interior features; (B) EcoUnit with earth-filled lower part, upper part equipped with illustrative vegetation.

Figure 2 Grassland (upper picture) and tree saplings (bottom picture) planted in EcoUnits of the iDiv Ecotron.

Figure 3 Experimental setup of the case study.

Figure 4 Effects of (a) aboveground invertebrate treatment (Control, Herbivores only, Coccinella low, Coccinella high; details in App.3) as well as (b) the interaction of belowground invertebrate presence (with/+ soil fauna, without/- soil fauna) and bean plant neighbor species identity (*Bellis perennis* L.*, Centaurea jacea* L., *Festuca pratensis* Huds.*, Holcus lanatus* L.) on the maximum number of aphids; (c) aboveground invertebrate treatment and (d) bean plant neighbor species identity on bean dry weight; and (e) the interaction of aboveground invertebrate treatment and bean plant neighbor species identity on the species richness of nematodes. *p = 0.05; **p <0.01; ***p<0.001. For detailed results see App.8.

Figure App.2: (A) Total light intensity (µmol/m²*s), 5 cm above the standard soil surface, at 36 locations within an EcoUnit, averaged over 24 EcoUnits, and (B) normalized deviations of light intensity at the 36 spots within an EcoUnit; normalization based on the highest measured average value of total light intensity (shown in (A)), highest value is set to 1. Five cm above the standard soil surface. Distance luminaire to backlighting layer 160 mm; outside corners are not included in calculations due to high edge effects inevitably created by the construction itself.

Data Availability Statement

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1001 The datasets generated for this study will be published through the iDiv Data Repository upon
1002 acceptance of this manuscript. The respective DOI will be provided.

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Competing Interest Statement

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1005 The authors declare no competing interests.

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