Web of interactions among diversity approaches to identify ecosystem essential variables: Negev Highlands case study

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Abstract. The concept of ecosystem diversity essential variables (EEVs) offers a foundation for ecosystem studies. Identification of EEVs continues to be a challenge in the field of ecology, due to the lack of a conceptual and applied framework. This paper develops a conceptual framework, offering theoretical foundation and a methodology for identifying EEVs, reflecting essential biodiversity and geodiversity variables. We start with a conceptual model of ecosystem essential variables linking biodiversity and geodiversity processes into ecosystem diversity as a web of interactions (WoI). The WoI components and interactions enable the identification of EEVs and their essentiality by relating interactions among diversities to variables that identify them. We tested our conceptual pass way by analyzing drivers and feedbacks of ecosystem processes in the Negev Highlands. Based on the general models and research of the Negev Highlands, we present four steps for EEVs: (1) developing a general conceptual model of the abiotic and biotic components of the ecosystem that links both biodiversity and geodiversity and their interactions; (2) testing the validity of the general model for a specific ecosystem to find out the hydro-geo-ecological drivers and feedbacks controlling ecosystem diversity; (3) constructing a WoI that adds to the regular analysis of an ecosystem as an interaction among geodiversity and biodiversity by breaking down the two components of diversities into subcomponent and their interactions; and (4) translating of the WoI components and interactions to EEVs. We suggest that EEVs should be related not only to the components but also to the interactions among diversities. These steps are essential for developing a scientific framework that allows for systematic identification of EEVs and justification regarding the final selection of the essential variables. We suggest that the approach can potentially be applied to all global terrestrial system.

Key words: biodiversity; cross-level interaction; ecosystem services; essential biodiversity variables; essential geodiversity variables; geodiversity; source–sink relationship.

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INTRODUCTION

The concept of essential biodiversity variables (EBVs) has been proposed as a simple framework for monitoring complex biodiversity dynamics in ecosystems in a meaningful way (Schmeller et al. 2017). The EBV approach assumes that a small set of biotic variables can characterize biodiversity change over space and time and will thus be relevant for both scientific understanding and management of the biotic components of ecosystems. Although the concept...
has contributed to the biodiversity paradigm, there are three main obstacles that prevent the integration of the concept into ecosystem studies: (1) the lack of a framework that links biodiversity with the abiotic diversity, which together determine ecosystem diversity; (2) the lack of precision when a variable is essential, because essentiality could only have been identified by detailed conceptual models of ecosystem processes and feedbacks where biodiversity and geodiversity play a critical role in the functioning of the system; and (3) the absence of EBVs as a system concept because EBVs are defined by diversity component variable, while we claim that ecosystem diversity is a system of both geodiversity and biodiversity that are interacting in a web.

This paper presents a complementary conceptual framework for EBVs that addresses the main limitations of the EBV framework in addressing ecosystem and biodiversity change. This framework refocuses attention to ecosystem processes and the interaction between biological and geological diversities in producing ecosystem characteristics. The alternative is a framework for identifying ecosystem diversity essential variables (EEVs) that integrate both EBVs and essential geodiversity variables. The framework depicts the web of interactions (WoI) that links biotic and abiotic state and flow variables that together induce ecosystem diversity, which is a WoI among diversities, and the web is the foundations of defining ecosystem diversity essential variables (Fig. 1).

Fig. 1 presents a conceptual model representing an ecosystem-based approach for integrating biodiversity and geodiversity and linking biotic and abiotic elements, whose interactions determine ecosystem functions. Biological elements are emphasized regarding their organization, which encompass the essential processes, functions, and interactions among and between organisms and their environment. The model thus highlights cross levels of organizations and their interactions among ecosystem, landscape, populations, and communities when addressing biodiversity.

As represented in Fig. 1, ecosystem diversity is an end product, which depends on many abiotic and biotic processes and their interactions. The geodiversity components, which are defined as the set of abiotic processes and features of Earth’s critical zone (lithosphere, atmosphere, hydrosphere, and cryosphere; Zarnetske et al. 2019), are driven by interactions among geomorphological, hydrological, climatological, and geological processes (Parks and Mulligan 2010). These interactions are also the source of physical resources for biota. The components include water, energy, space, and nutrients, and their distribution and abundance are variable in time and space. As such, concept of geodiversity encompasses the changes in resource availability across time and space (Brilha et al. 2018). Identification of geodiversity variables is essential for the selection of biodiversity variables, since geodiversity represents the spatiotemporal space of environmental conditions determining resource availability, which then partly determines terrestrial biodiversity development (Tukiainen et al. 2017). Geodiversity is further linked to biodiversity because a more diverse abiotic environment permits a broad diversity of niches with their energy, water, and nutrient variation. This enables species coexistence through niche partitioning (Hjort et al. 2015).

Biota, whose diversity is regulated by resource availability, is organized into four levels of organization, landscape, ecosystem, populations, and communities, and the cross-level interactions (CLI) between them. The cross-level organization, together with the abiotic process interactions, generates variability in biota, usually described as biodiversity. The two levels that directly relate to biodiversity on the species level are the community and populations levels. In our model, we relate the biodiversity at these two levels to the other hierarchical levels (i.e., ecosystem and landscape). Energy cycling and nutrient cycling that are essential to the survival of populations and communities are regulated at the ecosystem level. The landscape level contributes to biodiversity by providing a landscape mosaic consisting of patch diversity. All the above CLI should be taken under consideration while discussing biodiversity (as exemplified in Fig. 1).

Several studies describe the relationship between geodiversity and biodiversity. These studies describe geodiversity as a measure of environmental resource availability and variability (Parks and Mulligan 2010). This non-living complexity, geodiversity, is hypothesized to lead to complexity within the living world (i.e.,
Abiotic processes that determine geodiversity include climate, which is the source of precipitation and solar radiation, both of which regulate ecological system processes. Geomorphology (the physical features of the Earth’s crust) regulates over-ground water and soil flows, influences radiation balances, and creates surface heterogeneity, all of which influence soil hydrology and properties that support ecosystem functions (Räsänen et al. 2016). Geomorphology influences runoff connectivity and soil properties (van der Ploeg et al. 2018). Hydrology includes the relationship between rainfall–runoff and soil moisture, which influences water availability to all ecosystem components and affects the distribution of nutrients throughout the system. In essence, geodiversity is a variable that provides diverse resources in time and space for all biodiversity components (Korner and Spehn 2002, Dufour et al. 2006, Jacková and Romportl 2008).

This conceptual framework broadens the research on EBVs, which to date has not fully examined the relationship between abiotic environmental properties and their spatial–temporal variation (the geodiversity of an area) and their...
interactions with biotic properties and their spatial–temporal variation (the biodiversity of an area). This gap has limited our understanding of EEVs, which requires equal information on both abiotic and biotic diversities (Geijzendorffer et al. 2016).

In addition to the direct links between geodiversity and biodiversity via resources, geodiversity is a major control of the diversity of habitats. A more varied landscape consisting of diverse abiotic habitats will lead to a broader available niche space for species to exploit (Dufour et al. 2006). For the maintenance of biodiversity, more resources and more temporally variable resources permit a greater niche width and increased specialization within this niche for coexistence to occur.

Biodiversity dynamics in ecosystems are dependent on ecological system organization and reorganization, resulting in flows of energy and nutrients between organisms and their abiotic environment. Hierarchy theory shows that ecological system organization is the result of flows within and between hierarchical levels (Peters et al. 2007). In our scheme (Fig. 1), we refer to two types of hierarchical levels. Type 1 is level of organization, including population, community, ecosystem, and landscape; type 2 is the interaction among trophic levels, which include producers, consumers, and decomposers. We assume that these CLI are a main regulator of biodiversity.

The four levels of organization whose CLI determine ecosystem diversity include the following: (1) population, which refers to processes of interaction within species; (2) community, which refers to processes of interactions among species; (3) ecosystem, which refers to processes among species and their abiotic environment that are characterized by energy and material flows; and (4) landscape, which refers to interactions among ecosystem (patches) through source–sink relationships with regard to energy, material, and organism flows. The CLI induce the biota to be organized into trophic levels. The CLI and their organization of trophic levels are variable in time and space, resulting in ecosystem diversity.

We propose in Fig. 1 that defining ecosystem diversity as interaction between biodiversity and geodiversity is not enough for defining essential ecosystem diversity variables. We assert that diversities are interacting and form a WoI. We propose that only after understanding the diversity components and their interactions, it is possible to identify essential ecosystem diversity variables. We turn the interactions between biodiversity and geodiversity to a web of diversity interactions. In Fig. 1, we show a general model of web of diversity interactions, which include the following abiotic diversities: climate diversity that can be represented by frequency and magnitude of participation and temperature variability; rock diversity that represents various geological forms and their surface properties that has shaped by geomorphology; soil diversity that refers to various soil types and their organization into soil horizons. Within biotic diversities, we include species diversity, that is, the number of species in the area and their abundance; functional diversity that describes the function of species in relation to ecological processes; and genetic diversity that presents the long-term accumulation of genetic material within population and communities.

Our framework (Fig. 1) suggests that to identify ecosystem diversity essential variables (Guerra et al. 2019), we have to uncover the variables that enable to quantify the six classes of diversities, which are included in the web of diversity interactions.

To show our approach and the connection between our general model (Fig. 1) and a specific region, we analyzed the Negev Highlands ecosystems. Based on the analysis of the conceptual model and the tangible model of the Negev Highlands, we developed a general framework for selecting ecosystem diversity essential variables (EEVs).

**The Case Study of the Negev Highlands**

*Drivers of biodiversity and geodiversity in the Negev Highlands*

The Negev Highlands of Israel is well suited for testing our model (Fig. 1). Since the 1960s, research in this region has advanced theory and practice for understanding processes that link resources and biota to the relationship between biodiversity and geodiversity (Yair and Shachak 1982, Olsvig-Whittaker et al. 1983). There has been substantial effort dedicated to understanding the effect, for example, of water limitation on
drivers of biodiversity and geodiversity. Below is a summary of the main processes linking geodiversity and biodiversity that will later contribute to the selection of EEVs.

*The hydrological cycle and water redistribution: the primary drivers of ecological processes of the Negev Highlands*

Redistribution of rainfall via surface runoff water is the mechanism for regulating biotic functions across level of organizations. Biodiversity is maximized through the creation of soil moisture-enriched patches, and the ecosystem is considered to be at its highest ecological state, when geodiversity creates distinct patches within the landscape characterized by a high variation in soil moisture between them. Rainfall redistribution by runoff regulated by geodiversity produces a diversity of soil moisture-enriched patches that conserve water resources, prevent water loss, and facilitate the development of ecosystem and landscape diversity (Yair and Danin 1980, Yair and Shachak 1982, Olsvig-Whittaker et al. 1983, Yair and Lavee 1985, D’Odorico et al. 2007, Parolari et al. 2015, Shepard et al. 2015). The main determinants of the distribution and abundance of water-enriched patches are topography, geology, geomorphology, and soil structure, which are collectively considered to be geodiversity (Thomas 2012, Gray et al. 2013, Bradbury 2014). The structural diversity of geology and geomorphology of the Negev Highlands, by providing permeable and impermeable surfaces and directing overland and subsurface flows, is thus the main mechanism that regulates the overall water availability and its temporal and spatial variability in a source–sink dynamic. Rock surfaces that generate runoff are sources, and soil patches that facilitate infiltration are sinks.

Geomorphology structure interacts with rainfall frequency, magnitude, and intensity (pattern) determining the total amount of water resources available to the biota and its organization in trophic levels. Thus, the interactions between geomorphology structure and precipitation enable high biodiversity to develop, function, and adapt to conditions of low and unpredictable rainfall pulses in time and space (Ludwig et al. 2005, Urgeghe et al. 2010, Merino-Martín et al. 2012, Moreno-de las Heras et al. 2012).

The high spatial and temporal variability of water distribution in the landscape produces moisture sources and sinks and facilitates high diversity of herbaceous species, which are the principal species providing primary production and the basis of food webs in the Negev Highlands (Mulroy and Rundel 1977, Aronson et al. 1992, Olsvig-Whittaker et al. 1993, Ward and Olsvig-Whittaker 1993, Ward et al. 1993, Boeken and Shachak 1998, Gutterman 2000, Turkington et al. 2005).

Evolution and maintenance of high-moisture sink patches (hot spots of biological diversity) is the consequence of geo-hydro-ecological processes (Yair and Shachak 1982).

*Feedbacks regulating the processes in the Negev Highlands*

We propose that the ecosystems in the Negev Highlands are regulated by three coupled feedbacks.

1. The hydrological feedback: This feedback controls surface water flow that infiltrates to the soil patches (water accumulation) or leaks out of the system (water loss). When water accumulation processes occur, a richer ecosystem state is prevailing. Water flow is regulated by the dynamics of three species of ecosystem engineers (EE) which effect geodiversity: cyanobacteria (Eldridge et al. 2000), shrubs (Wright et al. 2006), and porcupines (Alkon 1999). Cyanobacteria engineer the extent of the biological soil crust, which determines the volume of soil accumulated in the patch, which in turn determines the water availability that supports the biota. The water accumulation processes are enhanced by shrubs that construct soil mounds that change micro-topography under their canopy, and by porcupines that dig pits and also affect geodiversity on a small scale. Both pits and mounds intercept runoff flow and accelerate water accumulation.

2. The pedological feedback: This feedback controls components of geodiversity by regulating soil accumulation and erosion, and it is closely associated with the hydrological feedback. When soil accumulation prevails and erosion out of the ecosystem declines, the ecosystem state supports high diversity.
Soil accumulation is the product of engineering by cyanobacteria and shrubs, which stabilize the dust input to the system and convert the dust into soil (Offer et al. 1998). Cyanobacteria engineer the ecosystem through the formation of biological soil crust. Biological soil crust generates semi-impermeable surfaces that stabilize soil and provide soil sources to all system organisms. Porcupine activity and isopod activity that produce easily erodible soil mounds enhance soil erosion by surface runoff water. The balance between soil accumulation and erosion determines geomorphology dynamics that construct landscape physical patchiness in terms of rock-to-soil ratio (Lin 2010, Li et al. 2012, Vogel et al. 2013). All the above processes represent a feedback that determines ecosystem diversity of the Negev Highlands.

3. The energy and material feedback: The hydrological and pedological feedbacks are the foundation for the energy and material feedback. They regulate the biotic-induced accumulation and loss of energy and nutrients incorporated into organic life that are the principal processes constructing the ecosystem state of the Negev Highlands. The hydrological and pedological feedbacks lead to the creation and availability of multiple niches. Multiple niches support high species and functional diversity that exploit soil moisture, distributed unevenly across the landscape, for primary production (Zaady et al. 1996, 1998, 2000, Ben-David et al. 2011, Maestre et al. 2012, Delgado-Baquerizo et al. 2013).

There are three main life-forms of producers in the Negev Highlands, which provide the energy base for ecosystem functions. These include annual herbaceous plants, woody species, and cyanobacteria (Olsvig-Whittaker et al. 1983). The first form is represented by high species diversity and functional diversity of forbs and grasses (Maestre et al. 2012), which is related to energy allocation between below- and aboveground biomass production (root-to-shoot ratio). The second form, woody species, is represented by a lower species diversity but higher standing biomass. Its functional diversity is related to its ability to concentrate soil moisture by its roots and by its high efficiency in water use. In addition, this group is an important geodiversity agent as it forms a patch mosaic that regulates water flow (Gilad et al. 2004). The third form, cyanobacteria, is characterized by low species diversity, but it can accumulate energy and recycling nutrients even during low precipitation events (Zaady et al. 1998). The three forms of the primary producers support the food webs that determine the diversity and productivity of the consumers.

The herbaceous community supports a species-rich insect community that together contributes to the energy accumulated among herbivores (Glazer et al. 1991, Ayal 1994, Ayal and Merkl 1994, Krasnov and Ayal 1995, Krasnov et al. 1996, Fattorini 2009). Key herbivores (in terms of biomass) that feed entirely on either cyanobacteria or shrubs include certain species of snails (Yom-Tov 1971, Shachak and Steinberger 1980, Shachak et al. 1981, Steinberger et al. 1983, Abramsky et al. 1990, Jones and Shachak 1990, Degen et al. 1992, Hermony et al. 1992, Ward and Slotow 1992).

In addition, the three life-forms of producers provide the energy and nutrients for decomposition processes. Composition enhances soil function that in turn increases primary production (Zaady et al. 1996, 1998, 2000, Ben-David et al. 2011, Delgado-Baquerizo et al. 2013).

The drivers and the feedbacks in the Negev that regulate ecosystem diversities are summarized and depicted in Fig. 2.

Fig. 2 depicts the main interactions between geodiversity and biodiversity components in the Negev Highlands. The geodiversity components are (1) rainfall related to climate, and (2) rock and soil spatial and temporal patterns (mosaic) related to geomorphology and geology. The dynamics of the hydrological and pedological feedbacks generate the spatial and temporal distribution of soil moisture, which links the two main processes that determine ecosystem diversity (i.e., geodiversity and biodiversity). Soil moisture is the main driver of the food web with all the diversities of species that form the three ecosystem components of producers, consumers, and decomposers. The qualities of the three components can be considered as a feedback to soil moisture, on the one hand, and support the...
activity of EE on the other. In addition, as indicated in Fig. 2, EE play an important role in controlling geodiversity by determining the rock–soil patch dynamics, by which it affects soil moisture to support the various levels of biodiversity. In Fig. 2, we added the EE as regulator of biodiversity as a separate group of functional diversity. The flow among the ecosystem components describes the producer–consumer–decomposer feedback (4) to soil moisture. The three ecosystem components determine the cross-level interactions among populations, communities, and landscape. Ecosystem engineers are the agents of the feedback between biodiversity and geodiversity (5). The functional interactions among the biodiversity and geodiversity components create ecosystem diversity. For detailed descriptions of feedbacks 1, 2, and 3, see text.

Another important process on the landscape level is the vegetation pattern formation, which determines the distribution of shrub patches either in the form of spot or in the form of banded vegetation (Gilad et al. 2004). Patterns of vegetation regulate source–sink relationship and the distribution of water-enriched patches. The patch mosaic of soil moisture is also an outcome of the interaction between runoff connectivity and vegetation pattern (Okin et al. 2009). The distribution of shrubs in space controls functional connectivity of runoff, that is, the length of the runoff pathway, which is dependent on the interactions between rainfall properties and vegetation pattern (Okin et al. 2015). When adding the landscape perspective to
ecosystem diversity, the processes of vegetation pattern formation and connectivity by runoff are revealed as essential for understanding ecosystem diversity.

According to our scheme, ecosystem diversity is an integration of geodiversity and biodiversity. Biodiversity and geodiversity are characterized by composing of various diversities and interactions among them. For example, geodiversity could be viewed as interactions among soil, moisture, and geological diversities. Biodiversity could be view as interactions among genetic, species, and functional diversities. Therefore, diversities could be representing as a Wol among diversities (Figs. 1, 3). In the next section, we develop a web of ecosystem interactions for the Negev Highlands.

An integrated conceptual model: web of interactions among ecosystem diversities

The processes and feedbacks of the Negev Highlands system (Fig. 2) can be translated into a complex causal model that links the various diversities of the ecosystem (Fig. 3). This is a novel approach that was not used before. Also, in studies referred to various biodiversities (Shachak 2005) no attempt was made to find the interactions between diversities as shown below. We suggest that the Wol approach is essential for selecting and prioritizing ecosystem diversity essential variables. The model is aimed at describing the most significant connections in the Negev Highlands among and between diversities as a network of consequential casual relationships. The model provides the essence of interactions among diversities and how they are linked to each other and describes the connections between the processes displayed in Fig. 2 and diversities displayed in Fig. 3. The link between Figs. 2, 3 is the translation of biodiversity and geodiversity interactions into one scheme that helps to identify the ecosystem essential variables in relation to ecosystem diversity. For example, if the water regime in the Negev is a consequence of interplay between two components of geodiversity, that is, rainfall diversity and geomorphology diversity, it implies that essential variables to take into account when looking for essential ecosystem variable are rainfall pattern and geomorphological pattern that both are diverse and interact.

In the Wol, we included 10 types of diversities as follows: rainfall diversity, which is driven by characteristics of precipitation pattern including amount, spatial distribution, duration, and frequency. Rainfall diversity, in addition to being a central driver of system dynamics, is main component of ecosystem diversity; dust deposition diversity, which is variable in time and space. Since dust is the main source of soil, its diverse deposition patterns, in conjunction with other functions, affect the diversity of soil. Its own diversity depends on the frequency and magnitude of dust deposition through time that regulates the distribution of soil in the landscape; surface property diversity is the result of the interactions between pedological and hydrological feedbacks, and they create the geomorphological landscape mosaic. The landscape mosaic is a fundamental component of geodiversity, and its diversity depends on rock-to-soil ratio and the spatial distribution of rock and soil in space and time (i.e., rock and soil mosaic); functional connectivity diversity is an important factor that determines the diversity of the length of the runoff pathway. The length of the runoff pathway is diverse since its length is regulated by the interaction between soil property diversity, rainfall diversity, and biotic diversity. This is also important since functional diversity affects two other diversities: soil moisture diversity and vegetation pattern; soil moisture diversity, as can be seen in Fig. 2, plays a major role in most of the other diversities. This is because soil moisture is the main link between biodiversity and geodiversity. Soil moisture characteristics are very diverse spatially and temporally in the Negev Highlands. The landscape patchiness, in addition to its geological properties, is a landscape composed of patches with diverse soil moisture qualities. The patchiness varies extremely across scales. All the diversities described above are considered to be components of geodiversity (Fig. 1), and they affect directly and indirectly the components of biotic diversity. The most obvious effect is the creation of vegetation pattern; vegetation pattern is very diverse since it depends on the interactions between surface properties, functional connectivity, and soil moisture. This diversity has been demonstrated to occur in spot, band, and hole patterns, and the patches comprising these patterns vary in size and in their distribution in
space (Gilad et al. 2004). All the above interactions create niche diversity. Niche diversity could be described by multiple dimensions, including surface properties, vegetation pattern, soil moisture, and functional connectivity. Niche diversity is the source of plant functional diversity, which includes diversity of species that function in different ways as producers in relation to resource availability and vegetation pattern. In addition, plants also function as EE and they modulate their environment via their canopy and roots; animal functional diversity is a response to plant functional diversity, vegetation pattern, and surface properties. The two most important functions are diversity of consuming processes and diversity of EE function, mainly related to soil disturbance. The plant and animal functional diversities connect to the microbe functional diversity that functions in many ways in decomposition and nutrient recycling processes.

EEVs refer to ecosystem diversity as a WoI among its diversity components is the roadmap to quantify the essentiality of each component. We assert that prevailing that approach to EV is only to identify them. The WoI method that we present here adds dimensions to the essential variables. First, it maps the relationships between the diversity variables, this represents a

Fig. 3. Web of interactions (WoI) among and between the diversity of components that links biotic and abiotic diversities in the Negev Highlands ecosystem. All the components and their interactions vary in time and space and together determine ecosystem diversity. The WoI model includes 10 types of diversities (for detailed description, see text).
global diversity concept such as geodiversity or biodiversity as a system of diversities. In the system of diversities, there are two components that define the degree of its essentiality: the position in the network and the strength of the relationships. Hence, we define essentiality as the relative role of a component in the WoI in determining ecosystem diversity. Therefore, if we would like to identify EEVs they should be related to WoI components. There are two ways to quantify the essentiality of ecosystem diversity: (1) network analysis (Ulanowicz 2004), which identifies the position of diversity component and its relation to other component; and (2) structural equation modeling (Lefcheck 2016) that could reveal the strength of the relationship between the components. To demonstrate how to calculate essentiality, we constructed a table that shows the relationship between WoI and EEVs (Table 1).

Table 1 summarizes the relationship between WoI components and EEVs. In the table, we described in the horizontal dimension the diversity components that are shown in Fig. 3. In the vertical dimension, we identify variables that can quantify the diversities of WoI. The table itself relates the WoI components to a measurable variable (mark as 1 in the table). As can be seen in the table, not all measured variables are related to all WoI components. We define essentiality in relation to the number of links between WoI and their measurable variables. Since we have 10 WoI components, we related the number of relationship as percentage of relationship; that is, if only seven relationships between the two diminutions were found, we quantified it as 80% essentiality. If all WoI components are related to the measurable component, we quantified it as 100% essentiality. We found that most of the essential variables except for dust deposition pattern and evaporation are good indicators of the components of WoI. In the table, our underlying assumption for essentiality is that the number of components of WoI that is related to essential variable defines its essentiality. For example, the essentiality of rainfall pattern and patchiness are each 100%; that is, they contribute to our understanding of all WoI components. The essentiality of evaporation, in contrast, is only 40%, as it contributes to our understanding of only a third of the diversity components. All the other components are between 80% and 90%. We contrast this table just as an example; of course, that network analysis or equation model analysis will lead to a better understanding of essentiality.

| EEVs          | WoI component | DDP | RFP | SP | FC | SMD | VP | ND | PFD | MFD | AFD | ESS  |
|--------------|---------------|-----|-----|----|----|-----|----|----|-----|-----|-----|------|
| Rock-to-soil ratio |               | 1   | 1   | 1  | 1  | 1   | 1  | 1  | 70% |
| Soil moisture |           | 1   | 1   | 1  | 1  | 1   | 1  | 1  | 90% |
| Soil surface topography |        | 1   | 1   | 1  | 1  | 1   | 1  | 70% |
| Topography    |               | 1   | 1   | 1  | 1  | 1   | 1  | 1  | 1  | 1  | 1  | 80% |
| Soil quality  |               | 1   | 1   | 1  | 1  | 1   | 1  | 1  | 1  | 1  | 1  | 80% |
| Rainfall properties: frequency, magnitude, intensity | | 1   | 1   | 1  | 1  | 1   | 1  | 1  | 1  | 1  | 1  | 100% |
| Surface runoff |            | 1   | 1   | 1  | 1  | 1   | 1  | 1  | 1  | 1  | 1  | 90% |
| Evaporation   |               | 1   | 1   | 1  | 1  | 1   | 1  | 1  | 1  | 1  | 1  | 40% |
| Patchiness    |               | 1   | 1   | 1  | 1  | 1   | 1  | 1  | 1  | 1  | 1  | 100% |
| Sp. richness: flora |          | 1   | 1   | 1  | 1  | 1   | 1  | 1  | 1  | 1  | 1  | 80% |
| Sp. richness: fauna |         | 1   | 1   | 1  | 1  | 1   | 1  | 1  | 1  | 1  | 1  | 80% |
| Food web      |               | 1   | 1   | 1  | 1  | 1   | 1  | 1  | 1  | 1  | 1  | 90% |
| Decomposition |               | 1   | 1   | 1  | 1  | 1   | 1  | 1  | 1  | 1  | 1  | 90% |
| Biotic productivity |           | 1   | 1   | 1  | 1  | 1   | 1  | 1  | 1  | 1  | 1  | 90% |
| Primary production |           | 1   | 1   | 1  | 1  | 1   | 1  | 1  | 1  | 1  | 1  | 90% |

Notes: DDP, dust deposition pattern; RFP, rainfall pattern; SP, surface property; FC, functional connectivity; SMD, soil moisture diversity; VP, vegetation pattern; ND, niche diversity; PFD, plant functional diversity; MFD, microbe functional diversity; AFD, animal functional diversity; ESS, essentiality; WoI, web of interactions.
DISCUSSION

Recent studies emphasize the importance of essential variables in relation to climate, geodiversity, and biodiversity (Pereira et al. 2013, Bojinski et al. 2014, Guerra et al. 2019, Zarnetske et al. 2019). A problem emerges as the selections of the variables are complicated by the presence of too many variables and the difference in their essentiality. In this paper, we suggest a systematic pathway for selection and prioritization of ecosystem diversity essential variables. Within the ecological arena, there has been an ongoing effort to define the subsets of ecosystem variables, most commonly focusing on EBVs. Despite the development of the EBV concept and its contribution to the development to ecosystem diversity essential variables, there are three main problems that prevent the integration of the biodiversity essential variable concept into ecosystem studies: (1) the lack of a framework that links biodiversity with the abiotic diversity, which together determine ecosystem diversity; (2) the lack of precision when a variable is essential, because essentiality could only have been identified by detailed conceptual models of ecosystem processes and feedbacks where biodiversity and geodiversity play a critical role in the functioning of the system; and (3) the absence of EBVs as a system concept because EBVs are defined by diversity component variable, while we claim that ecosystem diversity as shown in Fig. 3 is a system of diversities both geo and bio that are interacting in a web.

In this paper, based on viewing ecosystem diversity as a WoI between component diversities, we developed and demonstrated the application of a framework for addressing ecosystem diversity essential variables (EEVs). The framework is based on four steps.

Step 1: Develop a general conceptual model, as presented in Fig. 1, of the abiotic and biotic components of the ecosystem that links both biodiversity and geodiversity and their interactions to ecosystem diversity. This model can be used as a roadmap for any terrestrial ecosystem since (1) every ecosystem is dependent on the interactions between geomorphology–climate–hydrology and geology; (2) the aforementioned interactions determine the supply of resources such as water, energy, nutrients, and space in the ecosystem; (3) the resource distribution and abundance are variable in time and space and their interactions create geodiversity, which is the stage on which biota is organized into trophic levels and levels of organization, and (4) is composed of many components of biodiversity such as genetic, species, and functional diversity.

Our general model (Fig. 1) shows an example of the main components that should be taken into consideration when dealing with ecosystem diversity when conceptualized as a link between geodiversity and biodiversity. The important links between the above two diversities are emphasized in many recent papers (Parks and Mulligan 2010, Tukiainen et al. 2017, Zarnetske et al. 2019). However, very little attention has been given to their integration into a system framework such as in Fig. 1.

Step 2: Test the validity of the general model for a specific ecosystem as presented in Fig. 2. We analyzed the region of the Negev Highlands in Israel to find out the hydro-geo-ecological drivers and feedbacks controlling ecosystem diversity. Our analysis suggests that to understand the ecosystem components and interactions, we must refer to the relationship between geodiversity and biodiversity. Analysis of the framework highlights the important role of EE as agents of feedback processes. For example, rock-to-soil ratio is shown to be a landscape feature that is important as a controller of ecosystem processes and communities that create the trophic levels. The driver and feedback diagram (Fig. 2) is very important as a mediating step toward the identification toward the construction of WoI and identification of the EEVs. Traditionally, ecosystem models have emphasized the functionality of biodiversity in terms of energy flow and nutrient cycling. Our analysis emphasizes the importance of the interactions between geodiversity and biodiversity components.

Step 3: Constructing a WoI diagram (Fig. 3). This is a crucial step that adds to the regular analysis of an ecosystem as an interaction among geodiversity and biodiversity by breaking down the two components of diversities into subcomponent and their interactions. If we define diversity as a number of entities and the difference among the entities and their organization in time and space (Shachak 2005), then for the Negev Highlands we have been able to define 10 abiotic...
and biotic diversities that together produce the ecosystem diversity (Fig. 3). In our scheme, there are the conventional diversities such as niche diversity, and plant and animal functional diversities, which are related to species diversity and genetic diversity. But, we found that the driven forces, rainfall and dust deposition, according to their nature also represent diversity of inputs to the system. Both of them are diverse in relation to their frequency and magnitude. Also, surface properties are related to diversity of patches that regulate biotic component of diversity. The same can be implied to soil moisture as the entity soil moisture is very diverse and the diversity is applied to soil depth and soil moisture across the landscape. Functional connectivity is depending in the Negev Highlands on the length of connectivity pathway, which is very variable according to rainfall pattern (Okin et al. 2009). Therefore, functional connectivity is also a part of the diversity of the ecosystem. Vegetation pattern is also a diverse feature of the ecosystem since vegetation pattern can take different forms such as spot, stripe, bands, and holes (Meron et al. 2004). Each of the diversities will have a different effect on the ecosystem variables. As we have shown in Fig. 2, all the elements that contribute to ecosystem diversity are related to the components of the general model (Fig. 1); that is, they are related to all geodiversity components and resources and to all biodiversity components and the biota. We suggest that the nine components (excluding the dust) of diversity described for the Negev Highlands could be applicable to all terrestrial ecosystems. However, dust deposition is unique to systems in which soil properties are determined by windborne processes; in many systems, it could be replaced by soil diversity. Step 3 could be applied to any ecosystem. This is because every ecosystem functions due to interactions among diversities. All ecosystems are heterogeneous in relation to their abiotic and biotic components. Therefore, if ecosystem is defining as a system that functions due to feedbacks between a geological setting and biotic components all ecosystem could be presented by a WoI among diversities. This is a novel idea, but it is important due to its generality.

Step 4: This step implies to the translation of the WoI components and interactions (Fig. 3) to EEVs (Table 1). We suggest that EEVs should be related not only to the components but also to the interactions among diversities. This is because the WoI describe ecosystem functionality by interactions among diversities and EEVs should capture these interactions. Defining diversity just by components is unable to define the degree of their essentiality; however, relationship enables to define essentiality by determining the strength of relationship between the diversity components and EEVs. There are at least two ways to determine the strength either by network analysis (Ulanowicz 2004) or by structural equation modeling (Lefcheck 2016). The higher the strength between the components of the WoI and the EEVs, the higher is their essentiality. To our best knowledge, this is the first attempt to define essentiality related to the interactions among diversity components. It is of importance to define essential variables in various fields such as climate, biodiversity, soil, and of course ecosystem. This emphasis that a focus on diversity should go beyond components and should integrate interaction.

**Conclusions**

In this paper, we offer a conceptual framework for determining EEVs. The main assertion of this paper is that in relation to diversity, components of diversity alone are not able to distinguish between essentiality of diversity variables. We suggest a new way to overcome this obstacle by describing diversity as a WoI among diversities. Based on analysis of the Negev Highlands ecosystem, we suggest four-step procedure that can help in the identification of EEVs. The four steps linked geodiversity and biodiversity to the drivers and feedbacks controlling ecosystem diversity. The steps are based on two models: The first describes the interactions between geodiversity and biodiversity that produce ecosystem diversity, and the second describes ecosystem diversity as a WoI among the diversities of the first model. The last step was a translation of the WoI into EEVs essentiality.

Our scheme is based on theoretical consideration and on the knowledge of the structure and function of the Negev Highlands ecosystem. We assume that our approach is suitable with some modification to every terrestrial system. This is because all ecosystems share the same diversities
and their interactions that are included in the Wol but in various strengths in the interactions.

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