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Towards a systematics of ecodiversity: The EcoSyst framework

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Abstract

Background: Although a standard taxonomy of organisms has existed for nearly 300 years, no consensus has yet been reached on principles for systematization of ecological diversity (i.e., the co-ordinated variation of abiotic and biotic components of natural diversity). In a rapidly changing world, where nature is under constant pressure, standardized terms and methods for characterization of ecological diversity are urgently needed (e.g., to enhance precision and credibility of global change assessments).

Aim: The aim is to present the EcoSyst framework, a set of general principles and methods for systematization of natural diversity that simultaneously addresses biotic and abiotic variation, and to discuss perspectives opened by this framework.

Innovation: EcoSyst provides a framework for systematizing natural variation in a consistent manner across different levels of organization. At each ecodiversity level, EcoSyst principles can be used to establish: (a) an extensive attribute system with descriptive variables that cover all relevant sources of variation; (b) a hierarchical-type system; and (c) a set of guidelines for land-cover mapping that is consistent across spatial scales. EcoSyst type systems can be conceptualized as multidimensional models, by which a key characteristic (the response) is related to variation in one or more key sources of variation (predictors). EcoSyst type hierarchies are developed by a gradient-based iterative procedure, by which the "ecodiversity distance" (i.e., the extent to which the key characteristic differs between adjacent candidate types) is standardized and the ecological processes behind observed patterns are explicitly taken into account.

Application: We present "Nature in Norway" (NiN), an implementation of the EcoSyst framework for Norway for the ecosystem and landscape levels of ecodiversity. Examples of applications to research and management are given.

Conclusion: The EcoSyst framework provides a theoretical platform, principles and methods that can complement and enhance initiatives towards a global-scale systematics of ecodiversity.

KEYWORDS
biodiversity, complex gradient, continuum theory, ecodiversity, ecosystem, geodiversity, gradient, landscape, mapping, typology

1 | INTRODUCTION: THE ELUSIVE HIGHER LEVELS OF NATURAL DIVERSITY

The establishment of explicit principles for a universal, dynamic systematics of organisms (Linnaeus, 1753; Ruggiero et al., 2015), closely linked to evolutionary theory (Darwin, 1859; Huxley, 1942; Noble, 2015), represents a major landmark in the advancement of natural sciences (Nature, 2007). So far, a universal, complete systematics for the higher levels of diversity, such as ecosystems and landscapes, is still lacking (Keith et al., 2015, 2020). Attempts at systematizing variation at these higher levels have remained limited in scope, typically addressing either ecosystems or landscapes; the aquatic, terrestrial or non-anthropogenous realms; and/or restricted geographical areas (Keith et al., 2013, 2020; O'Neill, DeAngelis, Waide, & Allen, 1986). This variation is typically systematized either as a type system or as a set of "essential variables" (e.g., Pereira et al., 2013; Pettorelli et al., 2016), but rarely as a combination of both. Furthermore, most typologies for these higher levels take only one source of variation, typically vegetation, into account (Ewald, 2003; Faber-Langendoen et al., 2016; Whittaker, 1962). The few examples of systems that address several aspects of natural diversity at the same time (e.g., species composition and environmental conditions) have tended to be uncomprehensive, pragmatic, expert-based and designed to serve specific applied purposes (e.g., Connor et al., 2004; Davies, Moss, & Hill, 2004; Federal Geographic Data Committee, 2012; Keith et al., 2020; Leathwick et al., 2002; Sayre et al., 2020). A universal system for the higher levels should instead be holistic and based upon clear principles rooted in ecological theory.

Why is there now such an urgent need for a systematics of natural diversity above the population level? The diversity of life on Earth is of fundamental importance for the services on which prosperity, even survival, of human civilizations is conditioned (Diamond, 2005; Díaz et al., 2019). The footprint of humankind has reached a magnitude that, in the opinion of many, calls for recognition of a new geological time period, the Anthropocene (Crutzen, 2002; Ellis, 2015; Zalasiewicz et al., 2015). Drastic measures have been suggested in response to biodiversity loss and ecosystem degradation, as expressed in the Aichi targets (Convention on Biological Diversity, 2007), the 2030 and 2050 action targets (Convention on Biological Diversity, 2020) and the "Nature Needs Half" initiative for protection of half of the World's land and water (Locke, 2013). Conserving species by preservation of the geological diversity that gives rise to the diversity of their habitats ("Conservation of Nature's Stage"; Beier, Hunter, & Anderson, 2015) requires reliable knowledge about, and tools for description of, ecosystems and landscapes (Lawler et al., 2015). Accordingly, the need for systematically structured information about all aspects of natural variation is now greater than ever (Alahuhta, Toivanen, & Hjort, 2020; Dinerstein et al., 2017; Faber-Langendoen et al., 2014, 2018; Keith et al., 2015).

A comprehensive systematics of natural diversity might provide answers to fundamental questions in ecology, such as (cf. Keith et al., 2013; Sutherland et al., 2013): How many types of ecosystems and landscapes are there? Where can they be found, and why? How are they organized and how are they related? Which ecosystems and landscapes are rare, and which are threatened? What are the causes and consequences of commonness and rarity at each level of diversity? Which future ecosystem changes can be expected owing to ongoing changes in land use or climate?

What, then, has prevented development of universal systems for the higher levels of natural diversity, such as ecosystems and landscapes in Noss' (1990) hierarchy of biodiversity levels? We argue that progress in this field has been impeded by lack of theoretically well-founded principles and models for systematizing the vast complexity of natural variation at these higher levels, and by unclear definitions of basic concepts (O'Neill et al., 1986). Most importantly, ecosystems and landscapes do not comprise only organisms, but also include the environment, interactions within and between their living and non-living components, and the processes that give rise to variation in the structure and composition of these components (Swanson, Kratz, Caine, & Woodmansee, 1988; Tansley, 1935). We propose the collective term "ecodiversity" for these levels of diversity, which are qualitatively different from, and possess a complexity that extends beyond, biodiversity (Allen & Starr, 1982; Harper & Hawksworth, 1994). Just as the systematics of organisms explicitly takes evolutionary processes into account (Michener et al., 1970), a systematics of ecodiversity should arrange units by their characteristics in a way that, at the same time, explicitly accounts for the Earth systems processes that give rise to their diversity. The term "ecodiversity" dates back at least to Naveh (1994), who used it with a slightly different meaning. Note that our definitions of key concepts are given in Box 1, whereas definitions of all terms that are italicized when they first appear in the text are given in the Supporting Information (Appendix S1).

Expanding on ideas by Harper and Hawksworth (1994) we conceptualize natural diversity as an overarching but decomposable whole, with three *main aspects*: *biodiversity*, *geodiversity* and *ecodiversity* (Figure 1). Biodiversity addresses all biotic variation, whereas geodiversity encompasses all abiotic variation, including the lithosphere, atmosphere, hydrosphere and cryosphere (Zarnetske et al., 2019), within *Earth's critical zone* (i.e., the life-supporting, superficial planetary system extending from the near-surface atmospheric layers that exchange energy, water, particles, and gases with the vegetation and ground layers down through the soil to the deepest bedrock weathering fronts; Jordan et al., 2001; Richter et al., 2018). Accordingly, our concept of

BOX 1 Glossary of key terms (a more comprehensive glossary is given in Supporting Information Appendix S1)

Abiotic—the non-living chemical and physical environment that is not associated with living organisms.

Biodiversity—the biotic aspect of natural variation, on levels of organization from biotic communities via species and populations to genes, and the processes that give rise to variation in their structure and composition.

Biotic—associated with, or derived from, living organisms.

Complex landscape gradient (CLG)—abstract, continuous variable that expresses more or less gradual, co-ordinated change in a set of more or less strongly correlated landscape variables; in practice, used in a wide sense also including complex landscape factors.

Ecodiversity—diversity of units defined by biotic and abiotic components and their interactions, and the processes that give rise to variation in the structure and composition of these components.

Ecodiversity distance unit (EDU)—unit of compositional turnover of the key characteristic of an ecodiversity level along a complex variable in the key source of variation at this ecodiversity level.

Earth's critical zone—the life-supporting, superficial planetary system extending from the near-surface atmospheric layers that exchange energy, water, particles and gases with the vegetation and ground layers down through the soil to the deepest bedrock weathering fronts.

Elementary segment—one in a set of smallest intervals into which a complex gradient is divided; defined by universal criteria that apply across all major types.

Environmental complex gradient—abstract continuous variable that expresses more or less gradual, co-ordinated change in a set of more or less strongly correlated environmental variables (= complex gradient); in practice, used in a wide sense also including complex environmental factors.

General ecodiversity model—a theory of variation and relationships that applies to any ecodiversity level, with gradients in (an) ecodiversity level-specific key source(s) of variation and key characteristic(s) as predictor and response, respectively.

Geodiversity—the abiotic features of natural variation, including the lithosphere, atmosphere, hydrosphere and cryosphere, with diversity levels exemplified by minerals, bedrock and landforms, and the processes that give rise to variation in their structure and composition.

Key characteristic—characteristic of natural variation that provides response variables in an ecodiversity model for a specific ecodiversity level (e.g., species composition at the ecosystem level and landscape element composition at the landscape level of ecodiversity).

Key source of variation—source of variation that provides predictors in an ecodiversity model for a specific ecodiversity level (e.g., local environmental complex gradients in ecosystems).

Landscape element—natural or human-induced object or characteristic, including spatial units assigned to types at an ecodiversity level lower than the landscape level, which can be identified and observed on a spatial scale relevant for the landscape level of ecodiversity.

Local environmental complex gradient (LEC)—environmental complex gradient that expresses local variation.

Major environmental complex gradient—one among the few environmental complex gradients that account for most of the variation in species composition within a major ecosystem type that may be attributed to environmental variation.

Spatial unit—geographically delimited area or site.

Standard segment—one in a set of intervals into which a complex gradient is divided, which is made up by one, two or more elementary segments, each comprising at least one ecodiversity distance unit (EDU) of variation in the key characteristic within the major type in question.

Type—category in a system established with the purpose of systematizing variation, defined as an abstract ideal.

Type unit—category in a type system (e.g., at any level in a type hierarchy).

geodiversity encompasses the entire "environment", including soil and climate, whereas our ecodiversity concept addresses biotic and abiotic variation at the same time. The concept of *diversity* is used here as synonymous with variation, addressing the *composition* of concrete and physically observable *objects* (i.e., their *performance*, or "degree of presence"; Halvorsen, 2012), their *structure* (i.e., distribution in space and time) and their *function* (i.e., the processes that regulate composition and structure and the mechanisms involved in the action of these processes). Our diversity concept also includes immaterial characteristics, such as historical land use or forest continuity (Franklin, 1988; Noss, 1990).

Decomposition of natural diversity into biodiversity, geodiversity and ecodiversity (Figure 1) facilitates establishment of one hierarchy of well-defined diversity levels for each of these three main aspects. Examples of biodiversity levels are organisms and plant communities (phytocoenoses; Westhoff & van der Maarel, 1978), whereas minerals and bedrock are fundamental geodiversity levels (e.g., Gray, 2013). Spatial and temporal variation at each diversity

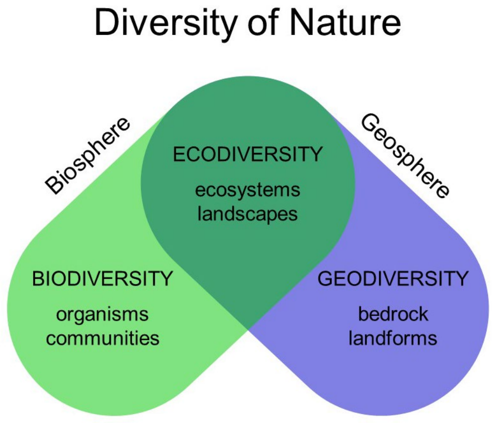

FIGURE 1 The three main aspects of natural diversity: the diversity of biotic characteristics (biodiversity); the diversity of abiotic characteristics (geodiversity); and the diversity of biotic, abiotic and combined characteristics (ecodiversity). Examples of diversity levels are given for each main aspect

level within each of the three main aspects can be organized into systems of abstract ideals, or *types*, which may, in turn, be organised in a hierarchically nested manner (Allen & Starr, 1982). The fundamental system of biodiversity types is the taxonomic hierarchy for the organism level, for which the defining characteristics are compositional, structural and functional (including phylogenetic) biotic properties. The degree of similarity in all relevant characteristics, interpreted with reference to evolutionary theory (e.g., Gould, 2002), underpins the well-established arrangement of organisms into a hierarchy with ≤ 12 formal levels (phylum, class, order, genus, species, etc.; cf. Ruggiero et al., 2015). Likewise, hierarchical taxonomies have been built for bedrock and minerals with internal logics consistent with geological patterns and processes (Mills, Hatert, Nickel, & Ferraris, 2009; Streckeisen, 1976). Concrete, spatially delimited areas (hereafter: *spatial units*) can be assigned to abstract *type units* of an existing type system by the process of mapping. We will use the term *type-hierarchy construction* for the process of building an abstract, hierarchical type system and the term *type assignment* for the process of assigning a spatial unit to an abstract type in such a system.

The main aim of this paper is to present a set of general principles for systematization of ecodiversity, based upon ecological theory. We accomplish this aim by: (a) outlining the basic properties of ecodiversity; (b) devizing principles and methods for sorting ecodiversity into compositional, structural and functional variation; (c) concentrating our ideas in a conceptual framework for ecodiversity systematics (EcoSyst), which facilitates description of ecodiversity by combining comprehensive sets of standardized descriptive variables (the *attribute system*) with type hierarchies (the *type system*); and (d) presenting "Nature in Norway" (NiN), a fully developed implementation of EcoSyst principles and methods for Norway, as proof of concept.

We approach the higher levels of natural diversity from basic ecological theory and concepts that apply to both aquatic and terrestrial realms, regardless of being "natural", semi-natural or "anthropogenous". We develop general principles, criteria and methods for organizing natural variation in a standardized manner by means of testable hypotheses emerging from a simple, general model. We argue that these steps, and the resulting value-neutral attribute and type systems, are important contributions towards the establishment of an urgently needed systematics of the higher levels of natural diversity. Our ambition is that the EcoSyst framework will encourage development of an evidence-based, universally applicable systematics for all observable aspects of ecodiversity, at spatial scales from microhabitats to landscapes.

2 | THEORETICAL FOUNDATION

2.1 | The primary ecodiversity levels

Organism, mineral and ecosystem are examples of fundamental levels in complexity hierarchies for biodiversity, geodiversity and ecodiversity, respectively. Being relevant for all of Earth's critical zone, including its marine, limnic and terrestrial realms, the landscape and the ecosystem are considered *primary ecodiversity levels*.

The many existing definitions of the *ecosystem* all emphasize systematic interactions between organisms, relationships between organisms and their environment, and processes that regulate these systematic interactions and relationships (Tansley, 1935; United Nations, 1992). Examples of type units that can be recognized at the ecosystem level are open fen, avalanche meadow and lime-poor semi-natural grassland. The ecosystem concept is flexible with respect to spatial scale and complexity, applying equally to a downed log, an extensive forest and a large lake (Gounand, Harvey, Little, & Altermann, 2018; Loreau, Mouquet, & Holt, 2003). In the way that forests contain logs, most ecosystems are aggregates of smaller, component ecosystems. For practical *land-cover mapping*, abstract ecosystem-type units are described that can be recognized at spatial scales typically between 1:5,000 and 1:20,000 (i.e., with minimum polygon sizes between 250 and 2,500 m^2). Ecosystem types relevant for this range of spatial resolutions reflect variation along local environmental complex gradients (e.g., Hemsing & Bryn, 2012; Ullerud, Bryn, Halvorsen, & Hemsing, 2018).

The topmost ecodiversity level is often referred to as the *landscape* level (e.g., Noss, 1990; Phillips, 2007), for which many different definitions exist (e.g., Forman & Godron, 1986; Matless, 2002). The definition of landscape adopted in EcoSyst comprises aquatic (i.e., freshwater and marine) and terrestrial realms. Examples of landscape elements are landforms, ecosystems and meta-ecosystems (ecosystem complexes). Type units that can be recognized at the landscape level as defined in EcoSyst are, for example, deep valley, rocky coast and inland alluvial plain. Landscape patterns can be approached from an organism-centric perspective, at spatial scales relevant for any organism (Wiens, Moss, Turner, & Mladenoff, 2007). Most landscape characterization and mapping efforts do, however, address the "landscape" as perceived

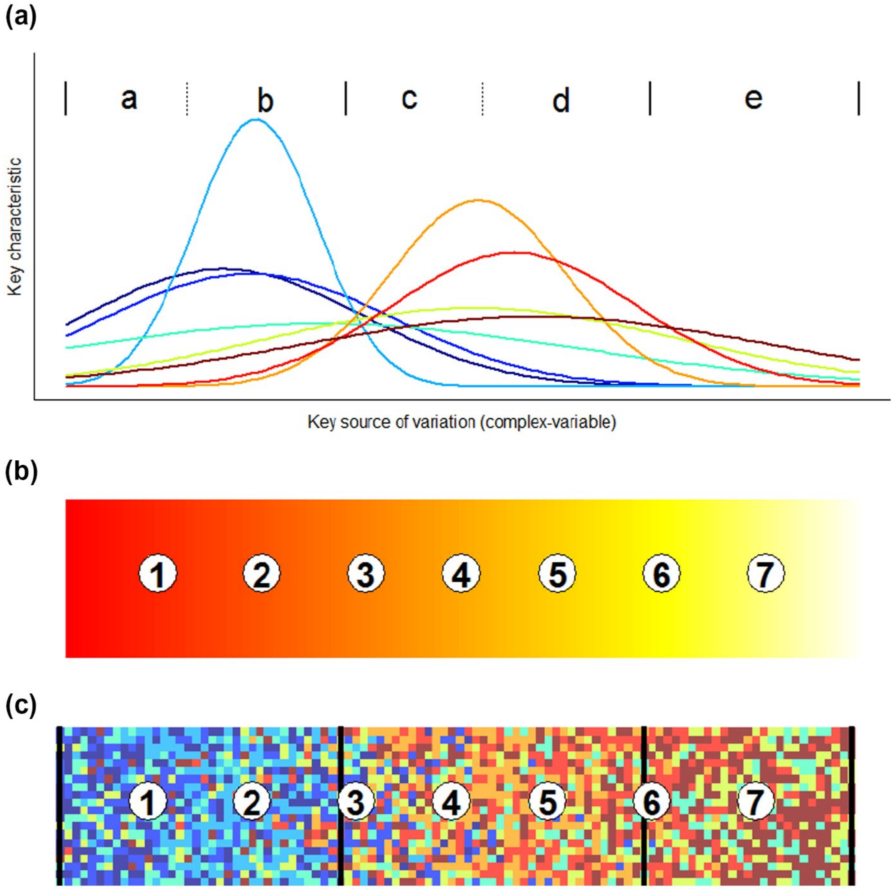

FIGURE 2 Illustration of the ecological continuum, underpinning the general ecodiversity model. (a) Generalized distributions of the abundance (aggregated performance) of eight species along a major local environmental complex gradient (e.g., soil acidity as expressed by pH). The vertical lines exemplify a division of the complex gradient into five elementary segments, a–e, which can be aggregated into three standard segments ab, cd and e (separated by continuous lines), each comprising similar amounts of species compositional turnover (further explanation in text). (b) Positions of seven observation units (1–7) in a hypothetical geographical space (i.e., on a map), onto which variation along the local complex gradient is illustrated by the transition from red (low pH) to yellow (high pH). (c) Presence of the eight species in (a) at different points (represented by pixels) in the geographical space in (b). The same colours are used in (a) and (c). Borders between elementary type units in the study area (c), indicated by thick lines, correspond to the bold vertical lines separating standardized segments ab, cd and e in (a). The relative frequencies of pixels of different colours in (c) accord with the species aggregated performance distributions in (a)

by a human observer, at spatial extents broader than those traditionally addressed in ecology (Council of Europe, 2000; Erikstad, Uttakleiv, & Halvorsen, 2015; Forman & Godron, 1986). Simensen, Halvorsen, and Erikstad (2018) recognize a gradient from a biophysical landscape concept that emphasizes the composition and structure of observable *landscape elements* to a "holistic" concept that emphasizes immaterial characteristics, such as visual perception and socio-cultural aspects. For practical landscape mapping, abstract landscape-type units are described that address the material, biophysical landscape, mappable at spatial scales 1:50,000 or coarser (i.e., with polygon sizes of 2–20 km^2; Erikstad, Halvorsen, & Simensen, 2019). Thus defined, landscape types reflect variation along gradients in the composition of landscape elements.

In general, ecological complexity increases in a nonlinear manner towards broader spatial and temporal scales (Allen & Starr, 1982; Loreau, Muquet, & Holt, 2003; McGill, 2010). Most landscape patterns result from processes that operate over longer time spans and affect broader spatial scales than ecosystems. Given that landscapes comprise complexity in addition to, and qualitatively different from, ecosystems, ecosystem-type hierarchies will not be nested within types in hierarchies of landscape types (Allen & Hoekstra, 1990). The independence of the two ecodiversity levels can be illustrated by the hydromorphological land-form sloping fen, which is typically covered by one spatial unit of one ecosystem type, open fen. One sloping fen might cross borders between delineated landscape types (e.g., between an undulating hilly landscape above and a wide valley landscape below the inflexion point in the valley side).

Provided that the primary ecodiversity levels are explicitly circumscribed with respect to the spatial domain and level of complexity addressed, *secondary ecodiversity levels* can be recognised for components and/or complexes of ecosystems in addition to landscapes. Examples of secondary levels are downed logs and tree stems, which host epixylic and epiphytic micro-ecosystems, and fjord landscape complexes, respectively.

2.2 | The ecological continuum

Quantum theory contributed strongly to progress in physics by provoking a shift from a continuous to a discrete view of key properties of Nature (Kleppner & Jackiw, 2000), whereas we argue that a shift in the opposite direction is required for progress in systematization of ecodiversity. At a first glance, this might seem counter-intuitive because the word "diversity" presupposes existence of discrete entities. Nature is, however, characterized by a multitude of biotic and abiotic properties that vary more or less independently in space and time (Gleason, 1926; Phillips, 2007; Zarnetske et al., 2019). This is exemplified by the continuous variation of species' *aggregated performance* in continuous environmental space (Figure 2a) in response to continuous environmental variation in geographical space (Figure 2b), typically observed as more or less continuous variation in species composition in geographical space (Austin, 2005; Curtis & McIntosh, 1951; Halvorsen, 2012; Figure 2c). We therefore argue that ecodiversity systematics should be built on continuum concepts like those originally developed for community ecology (Austin, 1985; Goodall, 1963; Whittaker, 1967).

At a first glance, the idea of a multidimensional ecological continuum appears incompatible with the idea of complex variation ordered in hierarchies of discrete types, which is an inherent property of human perception (Proffitt, 1993). Hierarchical systems of types are abstract, inherently unidimensional constructions that hide relationships among classes (Kalliola, 1939). Forcing a multidimensional network of variation into a hierarchy therefore inevitably entails significant loss of information (Gams, 1918; Tuomikoski, 1942). Furthermore, when continuous variation prevails at all ecodiversity levels, neither the levels themselves nor the types into which relevant objects are filed will be natural or concrete entities that can be recognized by objective criteria (Økland, 1990; Whittaker, 1962). Explicitly defined terms or units are, however, mandatory for communication of natural variation (e.g., via land-cover maps; Alexander & Millington, 2000). Reconciliation of the two approaches to sorting of natural diversity is nonetheless possible by a two-step procedure. Initially, the complex, mainly continuous patterns are identified and described; thereafter, the continuous, multidimensional network of variation is turned into types by dividing gradients into segments by transparent criteria (Økland & Bendiksen, 1985; Tuomikoski, 1942; Whittaker, 1962). As pointed out by Whittaker (1975), no one argues that words for colours should not be used because colours are subjectively distinguished fractions of a continuous spectrum.

2.3 | The gradient analytic perspective

Our platform for identifying and describing the predominantly continuous patterns of variation at the ecosystem level is the "gradient analytic perspective" (Halvorsen, 2012: pp. 12–13). This is a three-point summary of the core of *continuum theory*, a unified theory of biodiversity (Austin, 1999) that has been developed over nearly 100 years (Austin, 1985; Gleason, 1926; Whittaker, 1951, 1967). The gradient analytic perspective is a "theory" in the sense that it comprises a coherent system of ideas (Lawton, 1999), exactly like other biological theories, such as evolution of species through natural selection (Dawkins, 2009).

1. The abstract concept of the environmental complex gradient is appropriate for describing and understanding variation in the responses of species to the environment. External factors of importance for the abundance and distribution of species do not influence the species one by one, but act on the species in concert (Whittaker, 1967). *Explanatory variables* that account for variation along these external factors, on all spatial and temporal scales, tend to be correlated with other explanatory variables, forming *environmental complex variables*, defined as sets of more or less strongly correlated single environmental variables. Given that environmental variation is mostly continuous, we apply a broad definition of the *environmental complex gradient* (Whittaker, 1956), which also includes "complex factors" (i.e., variables that summarize naturally discrete variation).
2. Few major environmental complex gradients normally account for a large fraction of the total variation in species composition that can be explained by variation in the environment. Although the number of environmental complex gradients that might explain some of the variation in the abundance and distribution of organisms is essentially unlimited, studies of variation in species composition by ordination methods usually fail to extract more than three gradients in species composition that are interpretable in terms of environmental complex gradients (Økland, 1990). The term "major environmental complex gradient" addresses the few environmental complex gradients that, in each ecosystem, account for most of the variation in species composition that can be attributed to environmental variation.
3. Species are typically found within a restricted interval along each major environmental complex gradient. The range of genetic variation that can be maintained in a population of individuals that are able to exchange genes by normal mating mechanisms is limited. Accordingly, one of the most important ecological consequences of natural selection is that trade-offs are continuously made between beneficial traits that cannot be combined, such as large seeds and efficient wind dispersal (Tilman, 1990). Trade-offs impose ecophysiological constraints that limit every species to a restricted, species-specific tolerance interval along each major complex gradient. Within its tolerance limits, a species has positive fitness and, typically, a distinct optimum where its aggregated performance reaches a species-specific maximum value. The response curve for the species therefore tends to have a one-topped (i.e., unimodal) relationship with major environmental complex gradients (Figure 2a).

The gradient analytic perspective serves as the theoretical foundation for our conceptual model for variation at the ecosystem level of ecodiversity (i.e., our ecological model; cf. Austin, 2002). In this model, which we refer to as the *ecological space model*

(Whittaker, 1967), the aggregated performances of species are response variables, and major environmental complex gradients are predictors. The response of each species can be represented as a hypervolume (Hutchinson, 1957) or cloud (Whittaker, 1967) in the conceptual geometric space, with complex gradients as axes. The ecological space model serves as the theoretical foundation of several branches of ecological sciences (e.g., the expanding field of species distribution modelling; Araújo et al., 2019; Guisan, Thuiller, & Zimmermann, 2017; Halvorsen, 2012). This model recognizes the responses of species to complex gradients as "explained variation", whereas the residual "unexplained" variation represents stochastic components of variation in species performance. Demographic processes in the widest sense (van Groenendael, Ehrlén, & Svensson, 2000), including metapopulation dynamics (Hanski & Gilpin, 1991; Levins, 1969) and mass effects (Shmida & Wilson, 1985), are important sources of residual variation.

2.4 | A general ecodiversity model

The ecological space model and the gradient analytic perspective on which it is based can be generalized to a general ecodiversity model that is applicable to any ecodiversity level. This is accomplished by choosing other predictor and response variables than those of the ecological space model. In the general ecodiversity model, gradients in (an) ecodiversity level-specific key source(s) of variation replace the environmental complex gradients as predictors, while (an)other key characteristic(s) than species composition serve as the response (Figure 2a).

Candidates for key sources of variation at the landscape level (i.e., the axes of an ecodiversity model for the landscape level of ecodiversity, a *landscape space model*) are gradients of variation in topography and broad structural patterns of the terrain, underlying geological properties, such as bedrock and soil composition, hydrology, climatic conditions, composition of ecosystem types and intensity of human land use. Key characteristics at the landscape level (i.e., response variables of the landscape space model) are landscape elements that are observable at appropriate spatial scales (Simensen et al., 2018; Zarnetske et al., 2019). Like ecodiversity models in general, the landscape space model partitions variation into "explained" variation, resulting from geomorphological, ecological and anthropogenous processes (Zarnetske et al., 2019), and residual "unexplained" variation.

3 | ECOSYST: A FRAMEWORK FOR SYSTEMATIZATION OF NATURAL VARIATION

The EcoSyst framework is a coherent set of principles and criteria for building a systematics of ecodiversity, deduced from the general ecodiversity model which, in turn, operationalizes the gradient analytic perspective. The general ecodiversity model is the core of EcoSyst, but the framework also opens for recognition and systematic description of sources of variation other than the key source of variation and the key characteristic. Sources of variation are categorized into composition, structure and process (Supporting Information Appendix S3, Table S3.4). Examples of sources of variation filed under "composition" are species composition, which belongs to the biodiversity, and geological composition (e.g., minerals and bedrock), landforms and "man-made objects", which belong to geodiversity (Figure 1). "Structure" comprises local and regional environmental variation, in addition to short-term environmental variation, all of which belong to geodiversity (Supporting Information Appendix S2, Figure S2.2). The distinction between finer-scaled, so-called "local" (e.g., edaphic) variation and coarser-scaled, so-called "regional" (e.g., climatic) variation follows a long tradition in biogeographical ecology (cf. Cajander, 1921; Schimper, 1898; von Humboldt & Bonpland, [1807] 2009). "Processes" include fundamental evolutionary, geological and geomorphological processes in addition to the ecological processes that account for the response of biota to the environment.

The general ecodiversity model can be applied to any level of ecodiversity, thus addressing variation over a wide range of spatial and temporal scales (McGill, 2010; Willis & Whittaker, 2002). In principle, any source of variation can be selected as key source and key characteristic, but we emphasize a "basic EcoSyst set-up" (Table 1), which addresses the primary levels ecosystem and landscape, with local environmental complex gradients (LECs) and complex landscape gradients (CLGs), respectively, as key source of variation. The choice of local environmental variation as the key source of variation at the ecosystem level implies that variation at relatively fine spatial scales of (1–) 10–100 (–1000) m is addressed. This is the spatial scale at which most of the environmentally conditioned variation in species composition is accounted for; see Halvorsen (2012) and references therein. Although our description of EcoSyst will highlight this basic set-up, the framework as such applies equally well to other ecodiversity models, with other selected sources of variation. EcoSyst can, for instance, be parameterized with regional environmental variation as the key source of variation. An ecodiversity space with regional environmental complex gradients (RECs) as axes might account for coarser-scaled patterns, such as ecoregions (Bailey, 2014), biogeographical regions (Ahti, Hämet-Ahti, & Jalas, 1968; Moen, 1999) or other ecoregionalizations (Dinerstein et al., 2017; Keith et al., 2020).

The EcoSyst framework for systematization of natural variation builds on four cornerstones:

1. All phases of system development shall be characterized by reproducibilty, value neutrality and observer independence. Observer independence here implies transparency and repeatability in the sense that any person who accepts the method and the evidence is likely to reach the same conclusion (McHarg, 1969).
2. EcoSyst principles shall be based upon the general ecodiversity model, building on all relevant, available knowledge while at the same time avoid constraining legacies from other systems.

TABLE 1 "Basic EcoSyst set-up": ecodiversity models for each of the two primary levels of ecodiversity, with key sources of variation and key characteristics

Ecodiversity level	Definition	Key source of variation (predictor)	Key characteristic (response)
Ecosystem	A more or less uniform area, comprising all organisms, the total environment they live in and are adapted to, and the processes that regulate relationships among organisms and between organisms and the environment (natural, or dependent on or shaped by human activities)	Variation along environmental variables [referred to as local environmental complex gradients (LECs)], representing conditions that are typically more or less stable over centuries and that vary on spatial scales typically finer than 1 km (e.g., edaphic variation)	Species composition (i.e., the species that exist together within a relevant spatial unit), quantified by an appropriate species performance measure
Landscape	A more or less uniform area including multiple ecosystems, aquatic and terrestrial, characterized by its content of observable, natural and human-induced landscape elements (i.e., natural or human-induced objects or characteristics), including spatial units assigned to types at an ecodiversity level lower than the landscape level, which can be identified and observed on a spatial scale relevant for the landscape level of ecodiversity	Variation along complex landscape variables [referred to as complex landscape gradients (CLGs); i.e., summaries of the co-ordinated variation in: (a) geo-ecological characteristics, such as topography and broad structural patterns of the terrain, and the underlying geological properties, including bedrock and soil composition; (b) expressed climate-mediated variation (e.g., forested versus open, alpine areas); and (c) human land use, including both gradual and discrete variation]	Composition of observable landscape elements that occur within a relevant spatial unit, quantified by an appropriate performance measure

TABLE 2 The eight taxonomic principles of EcoSyst for systematization of variation (e.g., at primary ecodiversity levels, ecosystems and landscapes)

Number	Principle
1	Full thematic coverage (i.e., addressing all relevant sources of variation)
2	Full spatial coverage of the targeted area
3	An attribute system is constructed that consists of standardized variables for all relevant sources of variation
4	Ecodiversity models are translated into type hierarchies, one hierarchy for each ecodiversity level
5	EcoSyst type hierarchies are constructed by a criterion-based, repeatable, divisive (top-down) process, which results in discrete (non-overlapping) units
6	Each type hierarchy has three levels of generalization: major-type group, major type and minor type
7	Minor types are conceptualized as hypercubes of standard size in subspaces of the ecodiversity model space
8	A rule-based procedure facilitates aggregation of minor types to land-cover units that are adapted to mapping at specific spatial scales

3. EcoSyst concepts, terms, definitions and methods shall be independent of users (stakeholders of any kind, including sector authorities) and potential uses. This means that no a priori adaptation of the content of an EcoSyst implementation to specific material (e.g., aerial or satellite images), mapping methods (e.g., field-based mapping) or purposes (e.g., biodiversity conservation or impact assessments) shall be made.
4. EcoSyst shall include guidelines for land-cover mapping as an integrated part. In accordance with (3), these guidelines shall facilitate a posteriori adaptation of EcoSyst implementations to pratical use.

Building on these four cornerstones, a consistent, reproducible EcoSyst systematics for natural variation at each ecodiversity level is obtained by operationalization of the eight taxonomic principles outlined in Table 2.

Full thematic coverage (principle 1) implies that the EcoSyst framework shall facilitate standardized recording of any observable characteristic (object or property) of Nature. All sources of variation shall be covered, not only the key source of variation and the key characteristic addressed by the ecodiversity model. Full spatial coverage (principle 2) means that every location within a *target area* for implementation of EcoSyst (e.g., Earth, a continent or a part of a continent, such as a country) shall be assignable to a type in an EcoSyst type hierarchy.

Principle 3 implies that characteristics (objects, properties) that are observable at a given spatial scale, regardless of whether they belong to the selected key source of variation or key characteristic for the level-specific ecodiversity model or other sources of variation, shall be eligible for incorporation in the attribute system. The attribute system is a comprehensive set of standardized variables based upon explicitly defined terms that can be recorded on standard measurement scales. Examples of ecosystem-level attribute variables are the landform “solifluction lobe” and the short-term environmental variable “regrowth of semi-natural and strongly modified agricultural ecosystems” (for more examples, see Supporting Information Appendix S3). The former can be recorded as present or absent in a spatial unit, whereas the latter is recorded as a property of entire spatial units on an ordinal 1–5 scale.

Principles 4–7 provide guidelines for construction of EcoSyst type hierarchies. Principle 4 implies that variation accounted for by the level-specific ecodiversity models, and this variation only, is accommodated into type hierarchies. One type hierarchy is constructed for each ecodiversity level (Figure 3). An EcoSyst type hierarchy therefore expresses variation along the major complex gradients in the key source of variation, ranked by the amount of compositional variation in the key characteristic along each complex gradient. The basic EcoSyst set-up for the ecosystem level implies construction of one conceptual ecodiversity subspace model for each major type, with LECs, scaled in units of species compositional

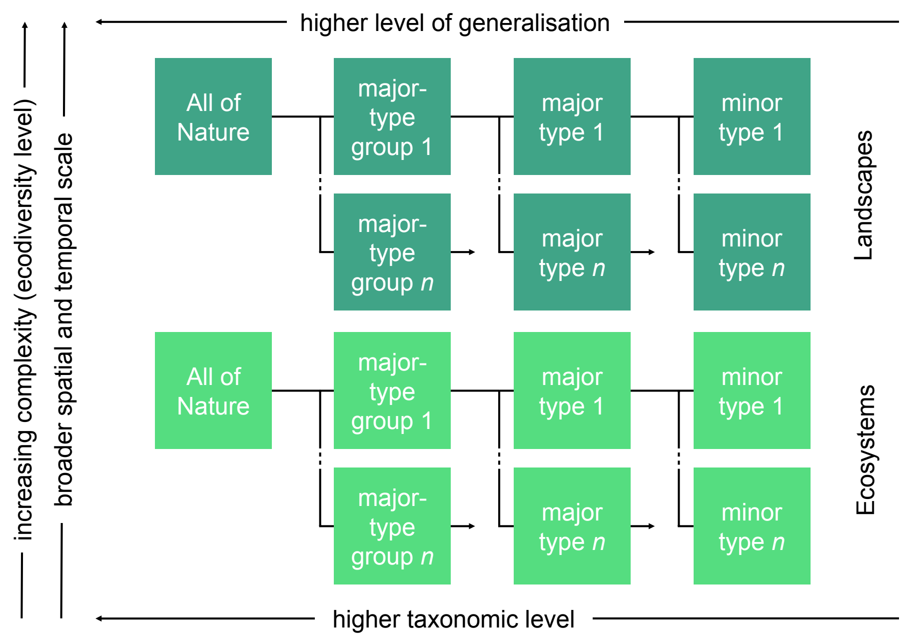

FIGURE 3 “Basic EcoSyst set-up”: hierarchies for the two primary ecodiversity levels, landscape and ecosystem, illustrated by a conceptual graph. At each of the two ecodiversity levels, a standard generalization hierarchy with (up to) three levels is constructed by applying the taxonomic principles listed in Table 2 and described further in the main text. The number of type units, indicated by *n*, can vary between generalization and ecodiversity levels. The arrows to the right of each major-type group and major-type box indicate that each type at these levels can be divided further. Examples of types for each combination of ecodiversity level and generalization level (also see Figure 5), are as follows: minor landscape type IA14, “undulating hills below the forest line”, which belongs to major landscape type “inland hills and mountains” (IA) in major-type group “inland landscapes” (I); and minor ecosystem type T1-1, “lime-poor open subxeric shallow-soil ground”, which belongs to major ecosystem type “open shallow-soil ground” (T2) in major-type group “terrestrial systems” (T)

variation, as axes (Figure 4). Likewise, the EcoSyst model for the landscape level is the landscape space model, with CLGs, scaled in units of variation in landscape element composition, as axes.

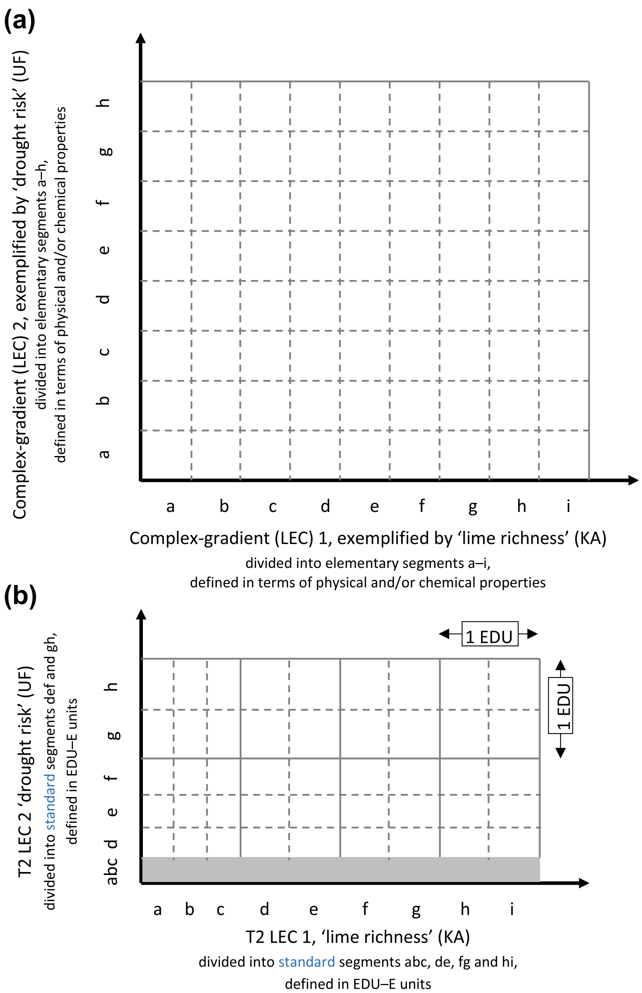

FIGURE 4 Two representations of a conceptual ecodiversity subspace model, exemplified by major ecosystem type "open shallow-soil ground" (code T2) in the NiN implementation of EcoSyst. (a) General model representation, with the two important local environmental complex gradients (LECs) in this major type, "lime richness" (KA) and "drought risk" (UF), as axes. In this representation of the model, the LECs are divided into elementary segments a–i for KA and a–h for UF, defined by universal (chemical or physical) criteria that apply across all major types (e.g., pH units for "lime richness", and soil moisture, measured after a long drought spell, for "drought risk"). (b) Major-type specific model representation, by which the two LECs are scaled in EDU–E (ecodiversity units in ecosystems; for details, see main text and Supporting Information Appendix S2). Estimates of gradient length (compositional turnover) for LECs KA and UF in major type T2 are between four and five, and between two and three EDU–E units, respectively. Accordingly, the elementary segments are merged into four and two standard segments, respectively, in T2. These are subsequently combined into 4×2 = 8 minor types. Standard segments and minor types are separated by continuous lines in (b). The grey rectangle in (b) shows that UF elementary segments a, b and c are incompatible with affiliation to major-type T2

Construction of an EcoSyst type hierarchy starts with the total variation in the selected key properties in the entire targeted area, which is successively divided into smaller and smaller units (principle 5). The resulting type hierarchy is a *nested hierarchy* [i.e., a hierarchy in which all units at lower levels can be generalized to, and are nested (contained) within, exactly one unit at the next hierarchical level; Allen & Starr, 1982]. Explicit criteria for each of the exactly three hierarchical levels (*major-type group*, *major type* and *minor type*; principle 6; Figure 3) secures consistency across ecodiversity levels and across hierarchical levels within each type hierarchy. This number of hierarchical levels is considered an optimal compromise between simplicity and transparency on the one hand and detail and completeness on the other. We argue that the resulting hierarchical type systems are well suited for basic scientific purposes and for land-cover mapping (e.g., Alexander & Millington, 2000) and other applied purposes, such as red-list assessment of ecosystems (e.g., IUCN, 2018), conservation planning (e.g., Beier et al., 2015; Sayre et al., 2020), landscape planning (Marsh, 2005) and sustainable harvesting of natural resources (Convention on Biological Diversity, 2007).

Types at the lowermost generalization level, the minor types, are obtained by rule-based gridding of conceptual ecodiversity *subspaces*, with one subspace for each major type (Figure 4a; principle 7). First, the length of each complex gradient (i.e., the compositional turnover of the key characteristic within the major type) is estimated in *ecodiversity distance units* (EDUs). Second, each complex gradient is divided into the maximum possible number of major-type specific *standard segments* (intervals along complex gradients), each of which by definition comprises at least one EDU of compositional variation (Figure 4b). Finally, minor types are obtained for each major type by using the segmented complex gradients to define a grid in the appropriate number of dimensions. Each minor type represents a "hypercube" in this subspace (Figure 4b). In cases of reduced turnover along a secondary complex gradient in response to, for example, extreme conditions along a primary complex gradient, hypercubes are amalgamated to achieve the required dimension. Thus, if the average dimension of the two "boxes" along LEC 2 for LEC 1 segment hi in Figure 4b is less than one EDU, the two boxes will be coerced into one minor type.

Standard segments comprise one or more *elementary segments*, indicated in Figure 4a by small letters a–i and a–h for complex gradients 1 and 2, respectively. Although the partitioning into major type-specific standard segments is made separately for each major type, the elementary segments are defined by universal criteria that apply across all major types. This makes it possible, for each major type, to define and name the standard major-type specific segments by use of terms that apply to any major type at the ecodiversity level in question.

EcoSyst type hierarchies are built by an iterative procedure that requires: (a) an initial model of the natural variation at the ecodiversity level in question (Figure 2a exemplifies this for the ecosystem level); (b) a quantitative methodology for operationalizing the general principles in Table 2; and (c) a standardized method for

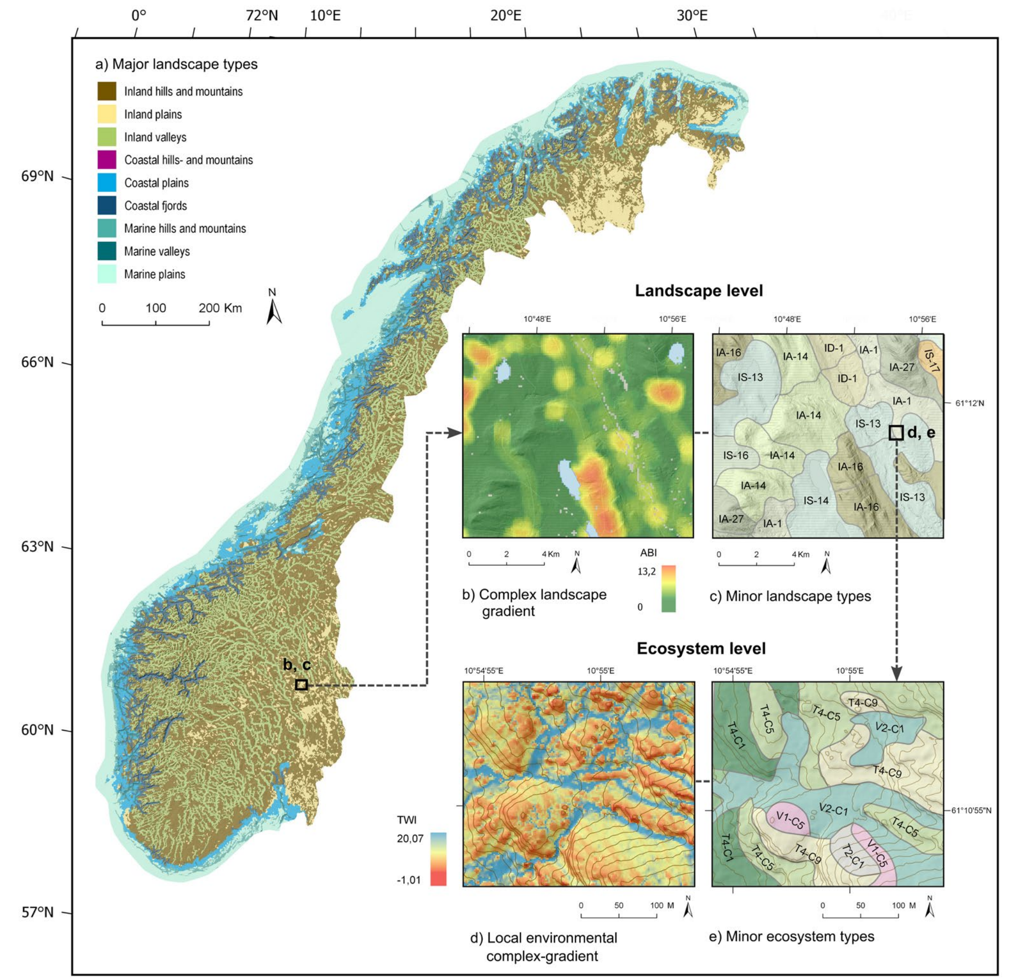

FIGURE 5 Selected examples from the NiN (Nature in Norway) implementation of EcoSyst principles. (a) Landscape level: major landscape types differentiated on the basis of broad-scale land forms and terrain variation. (b) Landscape level: variation along the complex landscape gradient (CLG) "land-use intensity" (ABI); one of the 11 CLGs for the key source of variation used to define minor landscape types, in the SE Norwegian area shown in (a). ABI expresses the intensity and extent of human land use in the landscape on a scale from virtually none via extensive to intensive. (c) Landscape level: map of major and minor landscape types for the same area as in (b). The major landscape types present in this area are as follows: inland hills and mountains (IA); inland valleys (ID); and inland plains (IS). Minor landscape types are defined by a combination of standard segments along CLGs, including ABI. Mapping-unit codes in (c) are explained in the Supporting Information (Appendix S8). (d) Ecosystem level: variation in the topographic wetness index (TWI) in the area shown in (c), which is dominated by forest (major ecosystem type T4; see Supporting Information Appendix S3). TWI is used here as a proxy for the local environmental complex gradient (LEC) "drought risk" (UF), which expresses variation in the risk of being exposed to episodes of extremely low soil moisture. (e) Ecosystem level: land-cover map for the area shown in (d) based upon field inventories, showing the distribution of mapping units adapted to scale 1:5,000 obtained by aggregation of minor ecosystem types (see Supporting Information Appendix S6). Mapping-unit codes consist of three elements; the major-type code (T2 = open shallow-soil ground; T4 = forest; V1 = open fen; V2 = mire and swamp forest); the scale code (C = 1:5 000 scale); and a code for mapping unit within each major type. This is exemplified by the code T2–C1 for T2 mapping unit C1 which, in this major type, equals minor-type T2–1 "lime-poor open subxeric shallow-soil ground" (see Supporting Information Appendix S5, Table S5.21). T2 minor types are defined by a combination of standard segments along the two LECs (for description of LECs, see Supporting Information Appendix S4) "lime richness" (KA) and "drought risk" (UF) as shown in Figure 4b

discretization of continuous variation based on assessment of ecodiversity distance (Figure 4; Supporting Information Appendix S2). The method for calculating complex gradient lengths in EDU units, using sets of *generalized composition data*, is a core element in the criteria that operationalize principle 7 in the EcoSyst framework (Halvorsen, 2015; Halvorsen, Bryn, & Erikstad, 2019; see Supporting Information Appendix S2). Together with specific criteria for how to perform the divisive process (principle 5) and how to delimit major types (principle 6), this method makes EcoSyst type hierarchy construction a repeatable, criterion-based process. Accordingly, an EcoSyst type hierarchy is a testable hypothesis that can be challenged, subjected to new tests with new data, and improved in an iterative manner (Supporting Information Appendix S2, Figure S2.6).

Following the recommendation of Whittaker (1962), we suggest that the number of qualitatively different categories of predictor (key source of variation) and response (key characteristic) in EcoSyst models are kept low for all ecodiversity models. Ideally, only one key source of variation and one key characteristic should be selected for each model. We recommend that the source(s) of variation that, at each ecodiversity level, account(s) for a major fraction of the total variation in the composition and structure of the prominent key characteristic are selected, in accordance with the "basic EcoSyst set-up" (Table 1). By intention, important structuring processes will then be accounted for at the same time by the models.

The minor types are adapted to land-cover mapping (principle 8) by successive, rule-based aggregation into mapping units that are appropriate for mapping at spatial scales ranging from fine to broad within the domain addressed at the ecodiversity level in question (Supporting Information Appendix S6).

4 | IMPLEMENTATION: NATURE IN NORWAY (NIN)

The "basic EcoSyst set-up" (Table 1) has been implemented for all land and offshore areas under Norwegian jurisdiction under the name "Nature in Norway" (NiN; Halvorsen, Bryn, Erikstad, Bratli, & Lindgaard, 2018; Halvorsen, Bryn, et al., 2019). In this section, we present selected features of the most recent version (v.2.2.0) of NiN to illustrate how the EcoSyst framework can be implemented for a target area. NiN v.2.2.0 includes fully developed type hierarchies for each of the ecosystem and landscape levels (Figure 3) in addition to a fully developed attribute system for the former. NiN v.2.2.0 is described in detail in the Supporting Information (Appendices S2–S8).

4.1 | Ecosystem level

The NiN implementation of EcoSyst for the ecosystem level of ecodiversity is based upon an ecological space model (Table 2; principle 2), which takes into account variation in the four *main ecosystem components*: terrestrial *ground*, marine and limnic *bottom* and waters, respectively, and snow and ice. The main ecosystem components correspond, to some extent, to the realms of Keith et al. (2020). The NiN v.2.2.0 ecosystem-type hierarchy addresses the variation in species composition (key characteristic) and its relationship to local environmental complex variables (LECs; key source of variation). Important ecological processes are recognized by categorization of LECs as "environmental stress gradients", "disturbance gradients" etc. (Supporting Information Appendix S4). The four main ecosystem components represent different domains of biodiversity that are linked to different aspects of geodiversity (Figure 1), display variation on different spatial scales, and have little overlap in species composition. All non-key sources of variation, including short-term environmental variation and quantitative variation in abundance of ecosystem components, are addressed by descriptive variables of the attribute system. Short-term environmental variation is exemplified by current land-use intensity and regrowth succession of tree stands (Table 2; principle 3; Supporting Information Appendix S3).

The NiN type hierarchy for the ecosystem level contains seven major-type groups, 92 major types and a total of 741 minor types (Table 2; principles 4–7; Supporting Information Appendix S5). Major-type groups include wetland and non-wetland terrestrial systems, bottoms and water bodies within each of the limnic and marine systems, and snow and ice systems. Each major type within each major-type group spans a subspace of the conceptual ecodiversity space, with its characteristic set of LECs as axes (Figures 4 and 5d; Supporting Information Appendices S2, S4 and S5). Major-type subspaces have to be convex in the sense that every point in the subspace can be connected to every other point by a straight line that is completely contained within the subspace. Examples of major types are "coral reef seabed", "euphotic limnic sediment-bed", "open shallow-soil ground" (Figure 4), "(non-wetland) forest", "mire and swamp forest", "open sea waters", "circulating lake waters" and "polar sea-ice". Typically, one to three (in exceptional cases ≤ 10) of the 57 LECs identified in NiN v.2.2.0 are considered important in each specific major type. LEC "lime richness" is used to define minor types in the largest number of major types, 40. Other examples of LECs include "strength of spring-water influence", "risk of drought" (Figures 4 and 5d) and "agricultural management intensity".

Within each major type, between one and 85 minor types were obtained by operationalization of principle 7 in Table 2 (i.e., by dividing the major-type specific subspaces into standard hypercubes; Figure 4b). The ecodiversity-level specific definition of the ecodiversity distance unit, the *ecodiversity distance unit in ecosystems* (EDU–E; Figures 4 and 5; for details, see Supporting Information Appendix S2), was defined as a difference in species composition of 0.25 proportional dissimilarity units (Czekanowski, 1909; Gauch & Whittaker, 1972). This corresponds to an exchange of about one-quarter of the species composition between opposite ends of an LEC segment (Figure 4b). The calculation of EDU–E, the division of LECs into standard segments and the subsequent identification of minor types (Figure 4) make use of generalised species composition data. Such data sets contain lists of all species regularly present in the species pool (Eriksson, 1993) of a community in a specific area.

The non-hierarchical attribute system (Table 2; principle 3) for the ecosystem level in NiN v.2.2.0 contains hundreds of variables that are organized into 10 categories by source of variation (Supporting Information Appendix S3, Table S3.4). Many of these variables are generic in the sense that they include one variable for each species, species group etc.

Guidelines for NiN-based land-cover mapping (Table 2; principle 8) form an integrated part of the NiN system (Bryn, Halvorsen, & Ullerud, 2018; Supporting Information Appendix S6). The minor types, which serve as mapping units at scale 1:500, are adapted to mapping at spatial scales of 1:2,500, 1:5,000, 1:10,000 and 1:20,000 by a process of successive aggregation (Figure 5e). By this process, the number of terrestrial mapping units is reduced from 448 minor types at scale 1:500 to 141 at scale 1:20,000. Furthermore, a methodology has been developed for mapping attributes by delineation of spatial units characterized by specific, pre-set values or exceedance of pre-set thresholds for the variables in question (Supporting Information Appendix S6).

4.2 | Landscape level

The NiN implementation of EcoSyst for the landscape level covers the Norwegian mainland and adjacent coastal areas (Figure 5a; Supporting Information Appendices S7 and S8; Erikstad et al., 2019). The NiN v.2.2.0 landscape-type hierarchy (Table 2; principles 4–7) rests on multivariate analyses of a comprehensive data set consisting of 85 quantitative variables, each representing a landscape element or property, recorded for 3,966 landscape units. The analyses support a top-down division into three units at the major-type group level [inland (I), coastal (K) and marine (M) landscapes], of which each of inland and coastal landscapes are divided into three or four major landscape types. Coastal landscapes include marine and terrestrial areas adjacent to and bordering on the coastline. Examples of major landscape types are "fjords" (KF), "coastal plains" (KS), "inland valleys" (ID) and "inland plains" (IS). Marine landscapes are tentatively divided into four major landscape types (Halvorsen et al., 2018): "marine hills and mountains", "marine plains", "marine valleys" and "the continental slope".

In accordance with principle 7, each major landcape type spans a convex subspace of the conceptual ecodiversity space, with its characteristic set of four to six CLGs as axes (Supporting Information Appendix S7). A total of 11 CLGs are described, of which eight are geological, geomorphological or geo-ecological (e.g., relative relief, variation from outer to inner coast, and occurrence of mire massifs and lakes), one represents climate-mediated variation (expressed as vegetation cover) and two quantify human land use (density of infrastructure and land-use intensity; Figure 5b). A total of 284 minor landscape types were obtained by discretization of major-type specific CLGs by a procedure similar to the one described above for the ecosystem level (Figure 4b), but using a landscape-specific definition of the EDU, the *ecodiversity unit in landscapes* (EDU–L).

The first-generation, computer-generated map of NiN landscape types for Norway, reproduced as Figure 5a (also see Figure 5c), is based upon the type system in the Supporting Information (Appendix S8) (Erikstad et al., 2019). A fully developed attribute system (principle 3) for variation at the landscape level has not yet been elaborated. As a preliminary solution, the 85 quantitative variables that were subjected to analyses are also used to characterize spatial units at the landscape level.

5 | DISCUSSION

5.1 | EcoSyst characteristics

We will highlight six characteristics of EcoSyst that make the framework suitable for building standard systematics for the elusive higher ecodiversity levels.

First, EcoSyst principles as summarized in Table 2 are built on basic ecological theory and concepts. Given that these principles are not limited to either aquatic or terrestrial realms, nor to specific ecodiversity levels, and because they apply equally to "natural" and "artificial" areas, EcoSyst is staged to meet the needs for description and analysis of the transformations our planet undergoes in the Anthropocene (Faber-Langendoen et al., 2014, 2018; Keith et al., 2015). Although the two primary ecodiversity levels, ecosystem and landscape, are explicitly pinpointed in the "basic EcoSyst set-up" and given particular attention in the present article, EcoSyst principles also apply to other definitions of ecodiversity levels. Thus, the level of ecoregions can be addressed by use of regional environmental complex gradients as the key source of variation, and secondary ecodiversity levels, such as epixylic micro-ecosystems, can be addressed by the same principles and methods as the primary levels. Furthermore, ecosystem complexes can be addressed by a change of the key characteristic from species composition to composition of ecosystems.

Second, EcoSyst is a set of general principles, criteria and methods for organizing natural variation in a standardized and value-neutral manner, and not a system of types per se. The EcoSyst framework thus combines the rigidity of a scientific approach with the flexibility offered by applicability to different levels of organization, different ecosystem components and different combinations of key characteristic and key source(s) of variation, in different geographical areas, in full or in an eclectic manner. The framework therefore meets universal in addition to specific (e.g., regional) demands and present-day in addition to future demands.

Third, EcoSyst implementations, such as NiN, are parameterized models of ecodiversity that can be tested and accepted or rejected (Halvorsen, Bryn, et al., 2019; see Supporting Information Appendix S2). EcoSyst type systems thus differ from almost all other global ecodiversity typologies proposed so far, which rest heavily on expert judgements (e.g., Dinerstein et al., 2017; Faber-Langendoen et al., 2016; Keith et al., 2020; Sayre et al., 2020). EcoSyst-based type systems can be developed and subsequently revised by an iteration process that opens for incorporation of new knowledge by a formal procedure that can be applied regularly or on demand (Supporting Information Appendix S2, Figure S2.6). Any candidate type system or part of such a system can be challenged and tested, provided that relevant data are available. This can be exemplified by a proposal for a new series of minor types within an existing major type, based upon an LEC that was previously regarded as subordinate. Estimation of species compositional turnover along this complex gradient by standard EcoSyst methods settles this case. The transparency and verifiability offered by EcoSyst substantially reduces the vulnerability to subjective decisions and shifts the role of experts from creators of expert-based type systems to solicitors of the knowledge on which these systems are based.

Fourth, EcoSyst principles circumvent the otherwise unresolvable dilemma of strictly type-oriented systems that a trade-off has to be made between a detailed system with an unmanageable number of types on the one hand and severe loss of information on the other

(Webb, 1954). EcoSyst meets this challenge by translating a simple ecodiversity model, which addresses only one or very few key sources of variation, into a type hierarchy (Table 2; principle 2). All other variation is taken care of in the attribute system which, in accordance with EcoSyst principles, is open-ended and can include variables for all observable objects or, in fact, all characteristics that can be observed or recorded in one way or another, quantitatively or qualitatively (Table 2; principle 3). Emerging global standards for measuring and monitoring of natural diversity [e.g., essential variables for biodiversity (EBV; Pereira et al., 2013), climate (ECV; Bojinski et al., 2014), geodiversity (EGV; Schrodt et al., 2019) and oceans (EOV; Constable et al., 2016)] can easily be taken as core elements of EcoSyst attribute systems.

Fifth, EcoSyst offers a spectrum of mapping strategies that serve different purposes. Selective mapping of EcoSyst types, attributes, or combinations thereof, is required for unambiguous identification of spatial units of a priori interest (e.g., that are targeted by legislation). Alternatively, wall-to-wall mapping can be performed according to value-neutral EcoSyst procedures before, and separated from, a posteriori value assessments. Regardless of the mapping strategy, EcoSyst-based land-cover maps do not escape general sources of uncertainty and error in maps (Eriksen et al., 2019; Ullerud et al., 2018). Continuous efforts for improvement of mapping practices and quality in mapping are therefore high-priority issues for further development of EcoSyst methodology (Bryn et al., 2018; Eriksen et al., 2019; Halvorsen, Eriksen et al., 2019).

Finally, EcoSyst opens for establishment of a database of unbiased ecodiversity map information by public authorities and/or by collaboration among stakeholders. EcoSyst-based mapping of variables and types assists the build-up of scientific knowledge in the first, descriptive phase of exploring a site, whereas EcoSyst has no role in the subsequent phase, in which these data are used to assess value-based goals and implement strategies and policies (Erikstad et al., 2008). The latter phase is carried out separately by each stakeholder or group of stakeholders with similar interests according to their specific value criteria. By careful planning of collaborative mapping programmes, two favourable targets can be reached in one operation: (a) that all information required by any stakeholder, translated into EcoSyst types and variables, is collected in one cost-efficient operation; and (b) establishment of a near-optimal basis for well-informed decisions in cases of conflicting land-use interests, such as conservation, cultivation, harvesting of natural resources or urban and regional development. The potential for efficient accumulation of knowledge by co-ordinated land-cover mapping was a major reason why the Norwegian Parliament sanctioned NiN as the national standard for describing and mapping ecodiversity in Norway (Parliament of Norway, 2015), later affirmed by a governmental white paper (Ministry of Climate and Environment of Norway, 2015).

5.2 | Challenges

A framework that shall serve as foundation for a universal systematics for the elusive higher levels of ecodiversity has to meet two requirements: first, that the principles and methods can be applied to the entire planet Earth and, second, that it is possible to fit the natural variation worldwide into one system. We are confident that the EcoSyst framework meets the first requirement. Theoretically, this is justified by the primary levels of ecodiversity (ecosystems and landscapes) and by the EcoSyst principles themselves being universal. From a practical point of view, this is substantiated by the successful implementation of EcoSyst for all of Norway (as documented above and in the Supporting Information), a country with extensive variation along latitudinal, elevational, topographic and land-use intensity gradients that cover variation from depths > 5,500 m below sea level to elevations of > 2,400 m and annual precipitation varying from *c.* 300 mm to > 5,000 mm (Bakkestuen, Erikstad, & Halvorsen, 2008; Moen, 1999). Given sufficient knowledge of the natural variation in a region, establishment of regional systems, such as NiN, by EcoSyst principles and methods is feasible. Furthermore, although the specific ecosystem- and landscape-type systems for Norway implemented in NiN v.2.2.0 are limited in scope, we see no reason why the experience gained during this implementation should not be transferable to any other part of planet Earth.

The second requirement, that the natural variation worldwide can be fitted into one EcoSyst-based system, is not obviously met. At present, this requirement appears to be more easily met for the landscape than for the ecosystem level because the “elements” that characterize landscapes, such as landforms (e.g., talus slopes, oxbow lakes and canyons), lakes, agriculturally improved land (e.g., fields and pastures) and infrastructure (e.g., roads, buildings and airports), are more universal and more widely distributed than the species that characterize ecosystems. Most variables that were used for the analyses underpinning the NiN landscape-type system are also relevant for other regions. Furthermore, data availability is rapidly increasing (e.g., as a result of the improved resolution and quality of remote sensors; Read et al., 2020; Zarnetske et al., 2019). The potential of remote sensing data for this purpose is exemplified by recently published global maps of physiographic features with fine-grained resolution developed by a joint venture among scientists (e.g., Sayre et al., 2014). The development of regional, continental or even global maps of landscape types based on the theoretical principles of EcoSyst thus appears within reach.

At the ecosystem level, higher-level types (major-type groups and major types) will be relevant for larger regions than lower-level types (minor types), simply because the former are more broadly defined. More fundamental than the types, however, are the LECs (see Supporting Information Appendix S4). The LECs reflect processes that vary from universal, such as the supply of mineral nutrients reflected by LEC “lime richness”, to regional or local, such as LEC “geothermal activity”. Accordingly, the spatial scales on which each LEC is relevant vary from global to local. We propose that the set of LECs addressed in NiN v.2.2.0 for Norway can be expanded to a set of global “essential LECs” and argue that global essential LECs can provide the platform required to overcome the major deficiency in current global ecosystem typologies, such as “World Ecosystems” (Sayre et al., 2020) and “Global Ecosystem Typology”

(Keith et al., 2020); the former lacks units on the lower generalization levels (cf. Figure 3) relevant for spatial scales at which practical management decisions are made, whereas the latter proposes that the two lowermost (fifth and sixth) hierarchical levels are filled with "units of established classifications". Applying EcoSyst principles and methods to global essential LECs may open for important innovation a consistent and rule-based appoach to establishment of types also at the lowermost levels in these global ecosystem typologies.

We recognize two major obstacles to the building of ecosystem typologies for continents or for the entire planet: one that is essentally biogeographical and one that is essentially practical. The biogeographical obstacle arises from the distance decay of compositional similarity (Nekola & White, 1999, i.e., that the species composition of sites with similar edaphic conditions become increasingly different with increasing inter-site distance). Experience from implementation of NiN shows that, for target areas of similar extent to the Norwegian mainland (*c*. 324 000 km^2, covering 13 latitudinal and 27 longitudinal degrees), regional complex gradients of the attribute system can be used to account for broad-scale compositional variation. At the scale of continents or the entire planet Earth, however, geographical variation in species composition is present that cannot be accounted for by bioclimatic variables (vicariance; Nelson & Rosen, 1981). Circumvention of this obstacle therefore requires a broadening of the key characteristic, which in NiN is species composition only. A strengthened emphasis on similarity in ecological structuring processes and functional-type composition, implemented in criteria for splitting or lumping major-type candidates into geographically vicariant major or minor types, might offer a partial solution (cf. Keith et al., 2020). A stronger focus on processes and composition of functional types might also increase transferability across regions or, more generally, to broader extents (cf. Cadotte, Arnilas, Livingstone, & Yasui, 2015; Powney, Preston, Purvis, van Landuyt, & Roy, 2014). The concept of ecoregions (Bailey, 2014) might be useful in this context.

The practical obstacle arises from mismatch between the current state of knowledge about the Earth's bio- and geodiversity and the heavy demands of EcoSyst type-hierarchy construction methods on such knowledge. The NiN implementation of EcoSyst has benefited strongly from > 200 years of biogeographical and ecological exploration of Norway, which is one of the countries in the World that is best equipped with relevant knowledge (gbif.org, accessed 1 March 2020). However, for most of the Earth our present knowledge of the biological diversity of most organism groups is far from sufficient to provide the data required by EcoSyst methods. Initiatives such as the Aichi targets (Convention on Biological Diversity, 2007) and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (Díaz et al., 2015), which strongly emphasize the essential role of knowledge generation in this field for the future of mankind (Díaz et al., 2019), will exert a constant pressure for acquisition of new knowledge. Furthermore, this process will be enhanced by developments in environmental DNA metabarcoding, which is about to become a standard tool for mass identification of cryptic taxa (e.g., bacteria and soil-dwelling and marine fungi; Rämä et al., 2016; Vik et al., 2013). In a few years, molecular methods might become a standard tool for characterization of community composition (Ruppert, Kline, & Rahman, 2019; Taberlet, Coissac, Pompanon, Brochmann, & Willerslev, 2012) and rapidly expand the empirical basis for construction of type systems for the ecosystem level by EcoSyst principles.

Lack of knowledge and data also applies to geodiversity, although statistical modelling is about to fill important gaps. This is exemplified by the SoilGrids250m data set, which provides global predictions for soil depth, pH, texture etc. at 250 m resolution (Hengl et al., 2017), and by improved digital elevation models obtained by airborne laser scanning (e.g., Murphy et al., 2011) and multibeam echo sounder (e.g., Erikstad, Bakkestuen, Bekkby, & Halvorsen, 2013). However, although the lack of wall-to-wall coverage of environmental information is an obstacle to mapping, construction of EcoSyst type hierarchies for the ecosystem level does not depend on such data. Identification of important local environmental complex gradients rests upon generalized knowledge emerging from case studies of species–environment relationships.

Finally, it is important to emphasize that the EcoSyst framework is staged for systematization of existing knowledge. Any EcoSyst implementation should therefore be regarded as a summary of the total available knowledge at the time it is published (i.e., as a hypothesis that can be tested and improved in an inductive manner). As such, EcoSyst might play important roles both in pointing out important knowledge vacancies and in filling them.

5.3 | Perspectives

Many specific questions have to be answered before the ambition to accomodate all of natural diversity into one system is within reach. Should ecodiversity levels other than, or in addition to, ecosystems and landscapes be addressed? Will incorporation of plant and animal functional type composition, in addition to species composition, as key characteristics facilitate development of a universal typology for the ecosystem level (cf. Harrison et al., 2010)? Are the scales of variation of interest at each ecodiversity level the same in different parts of the world? Which ecological processes are in need of being accounted for, other than those recognized as important in NiN? Can EcoSyst guidelines for land-cover mapping, implemented in NiN, be adapted to coarser resolutions than 1:20,000 and/or be implemented globally? Huge research efforts, including compilation and analysis of big data sets, will be required to answer these and other questions and to resolve upcoming challenges. Nevertheless, we see no reason why it should not be possible to overcome these obstacles by starting from first principles.

We argue that the standardized principles and criteria for a systematics of ecodiversity offered by EcoSyst might pave the way for important innovation. The stringent definitions and descriptions of types at each ecodiversity level make EcoSyst types well suited for ecoinformatics, because they can be implemented as classes in standardized environment ontologies, such as ENVO, and standardized gazetteers, such as GAZ (Buttigieg et al., 2013). This will facilitate consistent and efficient data handling, including the automated analyses of big data. New links across the biodiversity–geodiversity–ecodiversity pillars may thus be established. Likewise, variables of the NiN attribute system are well suited for harmonization with, and integration in, the sets of essential bio- and geodiversity variables that are currently under establishment (e.g., Feld et al., 2009; Pereira et al., 2013; Schrodt et al., 2019).

The NiN implementation of EcoSyst for Norway is established as a tool for research (e.g., Eriksen et al., 2019; Ullerud et al., 2018), management (e.g., red-list assessments of ecosystems; NBIC, 2018), environmental surveys (Framstad, Halvorsen, Storaunet, & Sverdrup-Thygeson, 2018; Norwegian Agriculture Agency, 2017; Norwegian Environment Agency, 2019) and environmental impact assessments (Norwegian Public Roads Administration, 2018). Planned uses of NiN include monitoring of land-use changes (Erikstad, Blumentrath, Bakkestuen, & Halvorsen, 2014), ecological accounting (e.g., Schröter, Remme, Sumarga, Barton, & Hein, 2014) and assessment of ecosystem condition (Nybø et al., 2017). We argue that a standardized systematics of ecodiversity will be useful for scientists by providing a reference frame for description, a consistent terminology of natural variation and numerous hypotheses that can be tested by experimental methods; for conservationists by summarizing relevant knowledge; and for planners and decision-makers by providing a transparent, value-neutral system and practical methods for land-cover mapping and description. Recent initiatives in conservation ecology, such as “Conserving Nature's Stage” (Beier et al., 2015), which addresses conservation of biodiversity via geodiversity conservation, explicitly call for an ecodiversity systematics based upon a combination of biotic and abiotic properties of nature.

The Anthropocene calls for a global systematics of ecodiversity based on integrative, interdisciplinary “Humboldtian” approaches (Schrodt, Santos, Bailey, & Field, 2019). Based on our experience with the NiN implementation of EcoSyst principles, we are confident that EcoSyst has the potential to play an important role in the development of a general systematics of ecodiversity. Such a systematics will allow us to address numerous intriguing basic scientific questions that have so far been possible to answer only for organisms.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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BIOSKETCH

The EcoSyst framework is the result of 14 years of work by the Geo-ecological (GEco) Research Group at the Natural History Museum of the University of Oslo. The work is carried out as part of the long-term "Nature in Norway" project for the Norwegian Biodiversity Information Centre (NBIC), which aims at providing Norway with a system for descriuption and typification of all Nature under Norwegian jurisdiction. Research interests of the GEco group include theoretical ecology, analysis and interpretation of patterns in the interface between biology and geology, plant population and vegetation ecology, distribution modelling, ecological climatology and methodological aspects of land-cover mapping.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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