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Variability of soil enzyme activities and vegetation succession following boreal forest surface soil transfer to an artificial hill

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Abstract

A landfill site in southern Finland was converted into urban green space by covering it with a layer of fresh forest humus transferred from nearby construction sites. The aim was to develop the 70 m high artificial hill into a recreational area with high biodiversity of flora and fauna. Forest humus was used as a source of organic matter, plant roots, seeds, soil fauna and microorganisms in order to enable rapid regeneration of diverse vegetation and soil biological functions. In this study we report the results of three years of monitoring of soil enzyme activity and plant species compositional patterns. Monthly soil samples were taken each year between June and September from four sites on the hill and from two standing reference forests using three replicate plots. Activities of 10 different enzymes, soil organic matter (SOM) content, moisture, pH and temperature of the surface layer were monitored. Abundances of vascular plant species were surveyed on the same four hill sites between late May and early September, three times a season in 2004 and 2005. Although the addition of organic soil considerably increased soil enzyme activities (per dw), the activities at the covered hill sites were far lower than in the reference forests. Temporal changes and differences between sites were analysed in more detail per soil organic matter (SOM) in order to reveal differences in the quality of SOM. All the sites had a characteristic enzyme activity pattern and two hill sites showed clear temporal changes. The enzyme activities in uncovered topsoil increased, whereas the activities at the covered Middle site decreased, when compared with other sites at the same time. The different trend between Middle and North sites in enzyme activities may reflect differences in humus material transferred to these sites, but difference in the succession of vegetation affects enzyme activities strongly. Middle yielded higher β-sitosterol content in 2004, as an indication of more intense plant impact. All reclaimed sites had characteristic plant species assemblages and parallel temporal changes, reflecting vegetation succession, occurred across all the sites. Rapid growth of vegetation on the covered sites restored the rhizosphere and contributed to the persistence of microbial activity. We suggest that transferring the surface soil humus layer is a useful approach for ensuring the outcome of habitat restoration and complementary habitat creation especially in situations where the source soil areas would otherwise be lost.

Keywords

landfill site, mineral soil, soil organic layer, soil enzymes, habitat creation, recreation, vegetation

Introduction

Land and soil use is drastically altered in a growing city, where new territory is needed for housing and for the infrastructure (Pavao-Zuckerman 2008). Novel approaches to enable distribution of soil removed from construction sites on the one hand and to provide green space for recreation on the other, are needed in limited urban space. Furthermore, the question of maintaining sustainable biological processes crucial for providing ecosystem services has recently been recognized important, also within urban areas (e.g. Isbell et al. 2011, Cardinale et al. 2012). Traditionally, surplus soils have been piled, thus mixing the different horizontal soil layers. However, as the biological activity is concentrated in the surface organic layer this procedure weakens soil fertility and recovery of soil functions. Healthy soil is dependent on diverse microbial consortia that have a fundamental role in the decomposition and transformation of organic matter (Kibblewhite et al. 2008). It has been estimated that more than 90% of the energy flow in soil systems passes through microbial decomposers (Nannipieri et al. 2003). The high biodegradation potential of microbial consortia is based on their vast enzymatic capacity. Enzymes involved in the degradation of macromolecules such as cellulose, hemicelluloses, starch and proteins are mainly extracellular and hydrolytic (Burns 1982, Tabatabai and Dick 2002).

Plant root and leaf litter is the primary source of soil organic matter and it affects the quality and quantity of carbon substrates and nutrients available to free-living fungi and bacteria. Helsinki City had constructed an artificial hill using mainly mineral soil removed from construction sites. As a novel approach to the various needs of landscaping, building of recreation areas and restoring biological diversity and functions through utilisation of surface soils removed from discontinued forest sites under constructional development, it was decided to collect the organic surface layer of forest separately and to use this biologically diverse material to cover a barren artificial hill. Fresh forest soil humus was distributed as a layer of a few tens of centimetres on a hill area, excluding steep slopes. The intention was to enhance the development of vegetation on the hill, to improve its recreational value and to restore biological functionality and ecosystem services through the increase in biodiversity (e.g. Forup et al. 2007, Hopwood 2008). However, it must be noted that the interaction of plants and microbes is disturbed when surface soil is transported to a barren hill constructed from stones and mineral soil, because symbiotic relationships and litter input are heavily affected (Gange and Brown 2002). Vegetation is drastically affected when trees are missing and, in spite of seeds and roots transferred within the humus material, local environmental conditions govern the persistence of transferred plant species and largely determine the trajectory of succession (Gibson and Brown 1991, Mortimer et al. 1998).

Habitat creation is potentially a very efficient tool for enhancing biodiversity in highly disturbed or completely artificial sites. The habitats being created are typically novel ones with plant and animal communities characteristically different from naturally occurring communities (Anderson 1995). Relatively few experimental studies have, however, been implemented on habitat creation in terrestrial environments, even though many projects have been performed to create compensatory habitats (Morris et al. 2006). Nevertheless, factors determining the expected patterns of vegetation succession are not known thoroughly enough to make reliable predictions (Vesk et al. 2008). The available species pool constrains the outcomes that are possible, but also soil type and properties are crucial in the re-vegetation process and largely determine the resulting community (Anderson 1995). Microbiota and soil invertebrate fauna can be regarded as an important soil property affecting vegetation development (De Deyn et al. 2003). Considerably better understanding exists about many aspects of habitat restoration and re-creation (e.g. Anderson 1995, Walker et al. 2004, Hedberg and Kotowski 2010), and most lessons learned in these contexts are also relevant in terms of habitat creation. Perhaps the most fundamental gain for biodiversity conservation, when these novel habitats are created, is the increasing connectivity of habitats and the decreasing risk of regional extinction of species using these habitats. In other words, species or immigration credit is produced (Hanski 2000).

The aim of our study was to monitor temporal changes in the enzyme activity and developing vegetation, and to compare the enzyme activity patterns in surface soil and plant species composition in order to reveal changes due to alteration in vegetation, as well as in litter quality and quantity and in physical conditions important to soil biota (moisture, temperature, pH). Regards to vegetation composition we hypothesize that vegetation succession should in the early phases be faster in moist depression (e.g. Grove) than in more exposed experimental sites (e.g. Top). On enzyme activities we hypothesize that (1) surface soil transfer decreases enzyme activities, (2) increase in vegetation supports enzyme activities in transferred soil and (3) plant species composition affects enzyme activity patterns. The enzyme activity pattern measured consisted of fundamental reactions in macromolecule degradation: arylsulphatase releases inorganic S, phosphomonoestarase and phosphodiesterase release inorganic P from organic molecules, and alanine and leucine aminopeptidases hydrolyze the amino-terminal from amino acids of peptides and some proteins. β-N-Acetyl hexosaminidase degrades chitin. Cellobiohydrolase and β-glucosidase are active in the degradation of cellulose into sugar monomers and β-xylosidase in the hydrolysis of xylo-oligosaccharides produced in the degradation of xylan. α-Glucosidase degrades starch. Soil ergosterol content is widely used as a measure of fungal biomass (Morgan and Winstanley 1997, Wallander et al. 1997). Because fungi in soil are important producers of extracellular enzymes and are probably affected by forest soil transfer, when ectomycorrhiza are no longer supported by trees, we also measured ergosterol content. β-Sitosterol, which reflects plant impact on soil, including litter, was also assayed (Sinsabaugh et al. 1997). Monitoring the changes in plant species composition are in wide-spread use in the studies of successional changes on reclaimed habitats and were also applied here to describe the general successional patterns on the experimental areas.

Methods

Study area and sampling

The study area is a former landfill site situated in Helsinki City, in the proximity of the Gulf of Finland. A total of about $5*10^6$ m^3 of mineral soil and non-biodegradable construction waste was transferred to the artificial hill site area of 38 hectares between 1990 and 2002. The organic surface layer of forest soil was distributed to the hill sites, excluding steep slopes and the hill top, in spring 2003. Heavy machinery (typical to mine industry and construction) was used for the collection, transportation and distribution on the soil cover. Due to the large-scale operation, characteristics of the humus material collected over large forest areas and level of mixing with mineral soil may have varied. Soil cover depth varied also, when organic material was spread over an uneven terrain. Middle and North sites were covered with surface soil from clear cut spruce forest and Grove was covered with clay and surface soil from an alder grove. Later Grove was planted with siblings of ash (*Fraxinus excelsior*) and hazelnut (*Corylus avellana*) from the site of the organic surface soil.

Three replicate 10 m × 10 m plots of four hill sites (Middle, North, Grove and Top) and of two reference sites were selected for soil microbial activity studies (Fig. 1, Table 1). Growing forests in the proximity of the sites of origin of the transported surface soils were used as reference sites (Alder for Grove and Spruce for Middle and North). Photographs of the studied sites at the onset of the study in June 2003, in August 2003, in August 2005 and after a decade in June 2013 are presented in electronic Supplementary Figures S1–S4. Soil samples were taken once a month from June to September each year from 2003 to 2005 as composite surface sample cores (depth 5 cm, diameter 3.4 cm) of 20 random subsamples from each plot. Samples were transferred to the laboratory refrigerated and were stored at +5 °C overnight. The next day, samples were passed through a 4 mm sieve.

Vegetation survey

For studies of vegetation composition, the abundance of all vascular plant species was surveyed in the same hill site (Middle, North, Grove and Top) replicate plots as

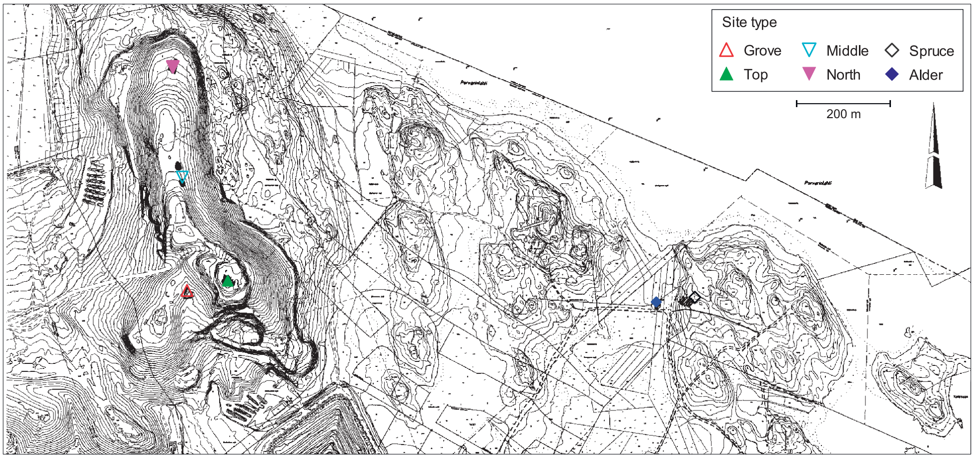

Figure 1. Map of the study area. The study area is situated in Helsinki City (60°13'N, 25°10'E).

Table 1. Characteristics of the sites monitored (see Fig. 1).

Site	Characteristics
Top	The top of the hill consisted of moraine. Vegetation was sparse but increased slightly during the monitoring.
Grove	Indentation on the southwest side of the hill. The bottom was covered with clay to prevent water infiltration and the clay layer was covered with surface soil from a black alder (*Alnus glutinosa*)-dominated grove in spring 2003. These two layers were not well separated and the surface soil contained variable patches of clay. Sparse vegetation of plants typical to the grove was observed during the first summer, but later the vegetation of different species dominated, e.g. very dense *Cirsium* growth.
Middle	Ridge site in the middle of the hill. Sandy moraine was covered with surface layer of old *Picea abies*-dominated forest. Vegetation was sparse during the first summer. Later *Agrostis* (2005), *Carex* (2004), *Luzula* (2004), *Poa* (2004) and *Rubus* (2004) species were common.
North	Ridge site in the north side of the hill. Sandy moraine was covered with surface layer of old *Picea abies*-dominated forest. Vegetation was sparse during the first summer. Succession later yielded very dense *Deschampsia* growth and in 2004 *Betula* (cut) and *Luzula* were common.
Alder	Old *Alnus glutinosa*-dominated brookside grove on the sea shore.
Spruce	About 60 years old *Picea abies*-dominated forest.

in the microbial activity study three times (late May, early July and early September) in 2004 and 2005. Plant abundance was estimated using a frequency method in which the number of positive records across sampling plots is summed and used to describe the commonness of a species. Here we applied this method so that each replicate plot was further divided into nine subplots and the number of subplots with positive records of a species was then used as the measure of abundance of vascular plants in plots (Greig-Smith 1983). Plants were identified according to Hämet-Ahti et al. (1998). We acknowledge here that the experiment was confined to a single landscape thus lacking spatial replications, and therefore generalization of the results to other areas should be cautionary. Subsamples taken from one treatment area

(Middle, North, Grove and Top) were combined before applying statistical tests to avoid pseudoreplication that may arise if spatial dependence of sampling is not accounted for (cf. Hurlbert 1984). However, all subsamples are shown in ordinations for enzyme and vegetation data (Fig. 3 and Fig. 5) to explore the total variation occurring in these data.

Physical and chemical measurements

The sieved samples were stored at +5 °C for 1 to 7 d before measuring dry weight, loss on ignition and pH_{KCl} in duplicate. For the measurement of soil dry weight and water content, fresh samples were dried at 105 °C overnight. Soil organic matter content (SOM) was determined by loss on ignition at 550 °C. For the pH measurement, 10 g of soil was weighed to 50 ml of 1 mol l^{-1} KCl solution in a screw cap bottle. After 10 min shaking at 200 rpm and settling for 2 h, pH was measured from the liquid phase using an Orion 550A electrode. Soil moisture and temperature were measured in the field at 5 cm depth on all the sampling dates from each plot at 20 random points using an HH2 Moisture Meter- instrument with a WET-sensor (Delta-T Devices Ltd). The means of 60 measurements for each site were calculated.

Ergosterol and β-sitosterol measurements

Samples were stored at +5 °C for 3 d and then, depending on the SOM content, 0.9 to 5.5 g aliquots were weighed into distillation flasks and 50 ml methanol (Rathburn, HPLC quality) was added and the suspensions were stored well capped at –20 °C until analysed for ergosterol and β-sitosterol. The slightly modified method of Sinsabaugh et al. (1997) was used: The total volume of methanol was made up to 100 ml before refluxing the samples for two hours. For saponification, 5 ml of 4% KOH in ethanol was added and the samples were refluxed for an additional 30 min. The undigested material was removed by filtration through glass wool. After addition of 10 ml of water into the methanol solutions the samples were extracted with three 10 ml portions of n-pentane (Merck) in separation funnels. The pentane of the samples was evaporated in a rotavapor (Büchi) and the solid residues were reconstituted in 1 ml of methanol before measuring the sterol contents by HPLC (Hewlett-Packard Model 1090 equipped with diode arrow detector and an analytical column of Hypersil ODS 200x2.1 mm with 5 µm particle size). Ergosterol was detected at 280 nm and β-sitosterol at 205 nm. Retention time for ergosterol was 6.9 min and for β-sitosterol 10.5 min when 50% methanol-water was used as an eluent with a flow rate of 0.4 ml/min. Quantitation was based on comparison of peak heights of sterols in the sample and in the standard solutions. A calibration curve was established for ergosterol (Fluka, purum 98%) from 0.6 to 46.5 µg/ml and for β-sitosterol (Sigma, S 9889, 98.3%) from 3.7 to 283.5 µg/ml.

Enzyme activity measurements

Enzyme activities were measured from 4 g samples stored in small plastic bags at –20 °C for 6 to 38 d (Wallenius et al. 2010) using ZymProfiler test kits (Vepsäläinen et al. 2004, Vepsäläinen et al. 2001). We measured the activities of arylsulphatase (no data for 2005), α-glucosidase (α-Glu), β-glucosidase (β-Glu), β-xylosidase (β-Xyl), cellobiohydrolase (Cell), β-N-acetyl hexosaminidase (Chi), phoshodiesterase (PDE), phosphomonoesterase (PME), and alanine- (AlaAP) and leucine aminopeptidases (LeuAP). Homogenized samples were suspended in 0.5 M acetate buffer at pH 5.5 and 1:100 dilutions (or 1:1000 dilutions for PME activities) were pipetted into multiwell plates containing pre-dried fluorogenic artificial substrates and incubated with shaking for 3 h at 30 °C. The fluorescence was measured with a Victor^2 multilabel analyzer (Perkin-Elmer) from four replicate wells on the plates. For the standardization, the curves of eight different concentrations of methylumbellipherone and for the aminopeptidases aminomethyl coumarine, in three replicates, were measured for each sample and dilution.

Statistical analyses

Multivariate ordination methods with non-metric multidimensional scaling (NMDS; see (Clarke 1993, McCune and Grace 2002) as implemented in the software PC-ORD, version 5.33 (McCune and Mefford 2006) were used to explore the main patterns of variation in enzyme activities and plant species composition between the experimental sites and their subplots. Quantitative version of the Sørensen (i.e. Bray-Curtis) distance measure was used to calculate the site-to-site dissimilarity matrix used in ordination, and varimax rotation was used in order to enhance correlation between the main component of variation and the first ordination axis (McCune and Grace 2002). The NMDS 'scree plots' were inspected to select the final number of axis dimensions included in the NMDS run (McCune and Mefford 2006).

We performed two NMDS runs with both the enzyme activity and plant species data, one with all the replicate samples handled separately and the other using monthly site means in the analysis but using otherwise similar settings. After performing the first NMDS run, Pearson correlations between axis scores for sites and environmental variables were calculated. Next, multiresponse permutation procedures (MRPP), a method designed for testing group-wise differences (Zimmerman et al. 1985), was applied as implemented in the software PC-ORD, version 5.33 to test whether sites belonging to different experimental treatments differed in ordination space. Quantitative version of the Sørensen (i.e. Bray-Curtis) index was used as distance measure in MRPP (McCune and Mefford 2006). Results from the second NMDS run were used to draw an ordination plot with successional vectors illustrating temporal changes in soil enzyme activity and plant species composition. Plant abundance measures were logarithmically transformed in the first NMDS in order to obtain a more stable solution.

Cluster analysis using Gower's coefficient and Ward's method was applied for enzyme activity data calculated per loss on ignition (SOM) using home tailored programs (ZymProfiler).

Results

Physical and chemical characteristics

The surface soils of the reference forests, with rather even terrain and trees providing shadow, were more moist, contained more organic matter and had lower temperatures than the hill sites (Table 2). Alder soil was not as acid as Spruce soil. Top site not covered by forest soil was driest, contained least organic matter of the hill sites and was less acid than forests and hill sites covered with forest soil. Grove was first covered with clay layer and then with surface soil from black alder (*Alnus glutinosa*)-dominated deciduous forest and the impact of clay is reflected as low organic matter content and moisture on the one hand, but as the highest pH of all the sites on the other. The two sites covered with spruce forest surface layer, Middle and North, were different: More mineral soil was mixed with the surface organic layer of spruce forest transported to North than to Middle and this was seen as lower moisture and organic matter content and higher pH than in Middle. The summer of 2003 was very warm in July, and especially surface soil temperatures on the hill were high.

Ergosterol and β-sitosterol contents

The samples were analyzed for sterols at the end of July and September in 2004 (Table 3). Both sterols had highest concentrations in soil of the reference forests, relatively high concentrations in Middle and less in North but low concentrations in Grove and Top, when calculated per soil dw. When calculated per SOM, the content of ergosterol was highest in the soil of reference forests, second highest in Middle and North, less in Grove and least in Top. The content of β-sitosterol was highest in the soil of reference forests and Middle, less in North and least in Grove and Top Pearson correlations between β-sitosterol and ergosterol were higher per dw ($r=0.84$, $n=33$) than per SOM ($r=0.62$), indicating differences in SOM quality. β-Sitosterol per dw correlated strongly ($r=0.96$, $n=33$) and ergosterol per dw also strongly ($r=0.90$, $n=33$) with SOM.

Enzyme activity and vegetation patterns

Enzyme activities per dry soil were clearly highest in the reference forest and lowest in Top not covered with forest soil organic layer (Fig. 2). Middle yielded higher activities

Table 2. Ranges and medians for each site and year for the physical and chemical characteristics.

		Water content %		SOM %		Temperature		pH_{KCl}	
Site	**Year**	**Range**	**Median**	**Range**	**Median**	**Range**	**Median**	**Range**	**Median**
Spruce	2003	33–48	43	37–46	40	10 -25	14	3.2	3.2
	2004	36–58	50	31–40	38	11–18	17	3.3–3.7	3.5
	2005	36–49	38	38–41	39	13–19	15	3.6–3.7	3.7
Alder	2003	39–54	43	34–39	37	10–24	14	3.8–4.0	3.8
	2004	51–64	58	39–47	42	11–18	16	4.1–4.3	4.2
	2005	45–61	52	41–49	44	14–20	15	4.3–4.6	4.4
Middle	2003	23–32	30	18–20	19	9.6–29	14	3.4–3.6	3.5
	2004	25–42	35	18–26	22	9.7–22	19	3.5–3.7	3.6
	2005	25–37	26	24–25	25	12–22	15	3.6–3.7	3.6
North	2003	11–20	16	6.5–7.9	7.0	11–30	15	3.9–4.0	3.9
	2004	10–25	19	7.0–12	7.4	11–23	19	3.9–4.1	4.0
	2005	12–20	16	6.4–8.0	7.4	12–19	15	4.1–4.2	4.1
Grove	2003	13–22	19	4.4–8.5	6.7	9.1–30	15	5.3–5.6	5.4
	2004	19–29	23	3.8–7.0	5.6	10–26	22	5.4–5.6	5.5
	2005	20–27	21	5.7–7.2	6.4	14–23	15	5.6–5.7	5.7
Top	2003	4.2–13	10	1.3–1.5	1.4	9.5–30	15	4.7–4.8	4.7
	2004	5.4–15	13	1.5–1.8	1.6	10–25	22	4.6–4.8	4.8
	2005	7.1–12	8.7	1.3–1.8	1.6	14–23	16	4.7–4.8	4.8

than North and Grove. PME activity was the highest in all the sites but the enzyme activity pattern was site-dependent. Middle had repeatedly the highest enzyme activities on the hill, clearly higher than North, which had lower SOM content and moisture but was less acid. Enzyme activities normalised by SOM content were used to reveal more sensitively the differences between sites and the possible temporal changes within SOM.

A two-dimensional solution was achieved with NMDS ordination for the enzyme activity data calculated per SOM (final value of the stress function = 9.50). A joint plot of the ordination for experimental sites is presented in Fig. 3. Axis 1 represented 87.7% of the variation of distance measures in the original data set, and axis 2 represented 8.0% of the variation. According to an MRPP analysis, the experimental treatments were separated in the ordination space ($p < 0.001$). Furthermore, pair-wise comparisons by MRPP showed that all treatment groups were differently ($p < 0.001$) distributed in the ordination space, with Top and Middle treatments being the most distinct and Spruce and Alder treatments showing some resemblance (Fig. 3). The vectors of the three most important environmental variables, SOM (loi), dry weight and soil pH (pH_{KCl}), were correlated to axis 2 so that SOM showed a positive correlation ($r = 0.62$) and dry weight and soil pH (pH_{KCl} negative correlations ($r = -0.58$ and -0.53, respectively). This observation indicates that these environmental variables formed a gradient parallel to axis 2 that correlated with the observed variation in enzyme activity patterns.

Table 3. Ergosterol and β-sitosterol (μg/g) in soil in 2004. Standard deviations in parentheses.

		Per dw		Per SOM	
Site	**Date**	**Ergosterol**	**β-sitosterol**	**Ergosterol**	**β-sitosterol**
Spruce	July 27th	38 (±7)	139 (±27)	127 (±26)	468 (±102)
	Sept 27th	75 (±22)	236 (±74)	199 (±52)	605 (±84)
Alder	July 27th	37 (±14)	203 (±159)	99 (±12)	472 (±149)
	Sept 27th	49 (±32)	275 (± 222)	100 (±37)	518 (±183)
Middle	July 27th	14 (±7)	138 (±95)	54 (±6)	487 (±96)
	Sept 27th	15 (±8)	130 (±76)	68 (±5)	551 (±140)
North	July 27th	3.6 (±1.0)	20 (±6)	48 (±5)	262 (±38)
	Sept 27th	4.0 (±2.2)	27 (±10)	56 (±26)	382 (±98)
Grove	July 27th	1.6 (±0.5)	8.4 (±1.2)	30 (±5)	163 (±22)
	Sept 27th	1.4 (±0.3)	6.1 (±2.3)	38 (±10)	162 (±68)
Top	Sept 27th	0.3 (±0.2)	3.0 (±3.0)	18 (±5)	145 (±89)

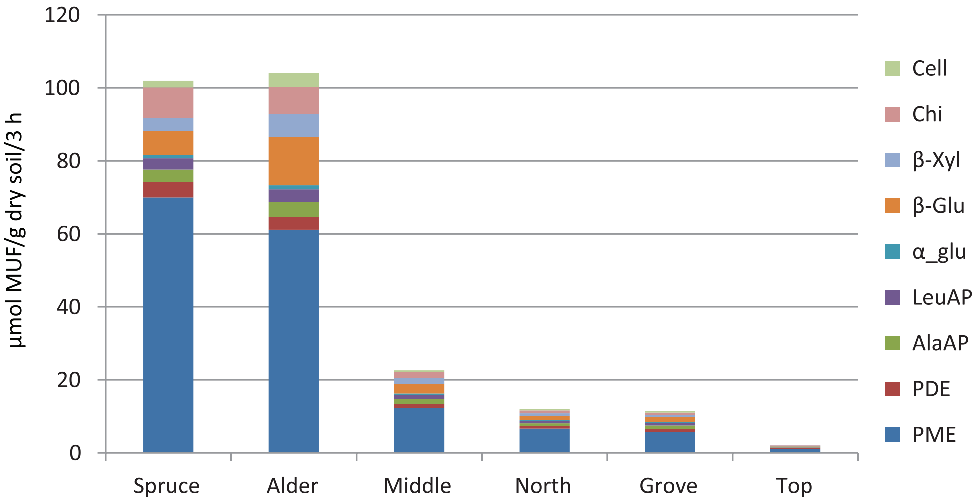

Figure 2. Sums of different enzyme activities in different sites per soil. Medians in three replicate plots calculated per dw from June to September in 2003, 2004 and 2005.

A two-dimensional solution was also achieved with NMDS ordination including monthly means of within-site replicate plots of enzyme activities (final value of the stress function = 8.75). Successional vectors joining monthly samples of different sites (i.e. experimental treatments) showed directional changes in two sites, with Top site moving closer to Grove and North and Middle gradually diverging from the other areas (Fig. 4).

A three-dimensional solution was achieved with NMDS ordination for the plant species composition data (final value of the stress function = 10.52). A joint plot of the ordination for experimental sites is presented in Fig. 5. Axis 1 represented 19.4% of the variation of distance measures in the original data set, axis 2 represented 29.8%

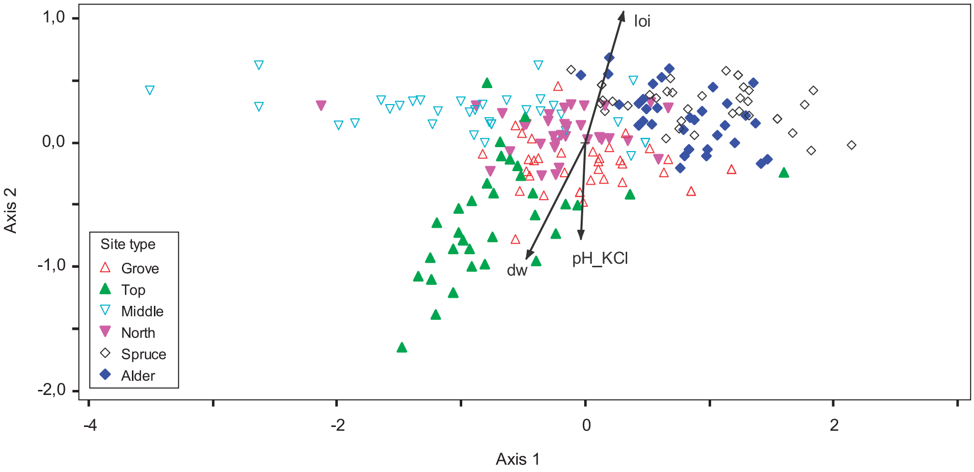

Figure 3. The joint plot of NMDS ordination for enzyme activity per SOM. All replicate plots of each study site with samples taken in June, July, August and September in 2003, 2004 and 2005. The vectors of environmental variables with strongest correlation to ordination axes (r > |0.5|) are shown.

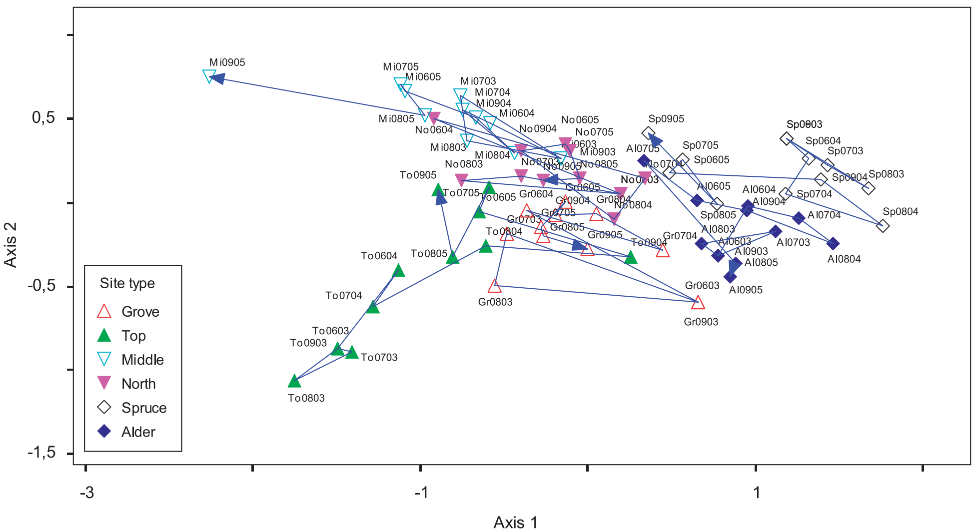

Figure 4. The NMDS plot showing temporal change in enzyme activity per SOM. Successional vectors joining the monthly means of replicate samples of each study site (i.e. experimental treatment) taken in June, July, August and September in 2003, 2004 and 2005. Point labels show two initials of the site, sampling month and year (e.g. Gr0603 = Grove June 2003).

and axis 3 represented 32.9% of the variation. According to an MRPP analysis, the experimental treatments were separated in the ordination space ($p < 0.001$), and pair-wise comparisons by MRPP showed that all treatment groups were differently ($p < 0.001$) distributed in the ordination space in years 2004 and 2005, with Top and

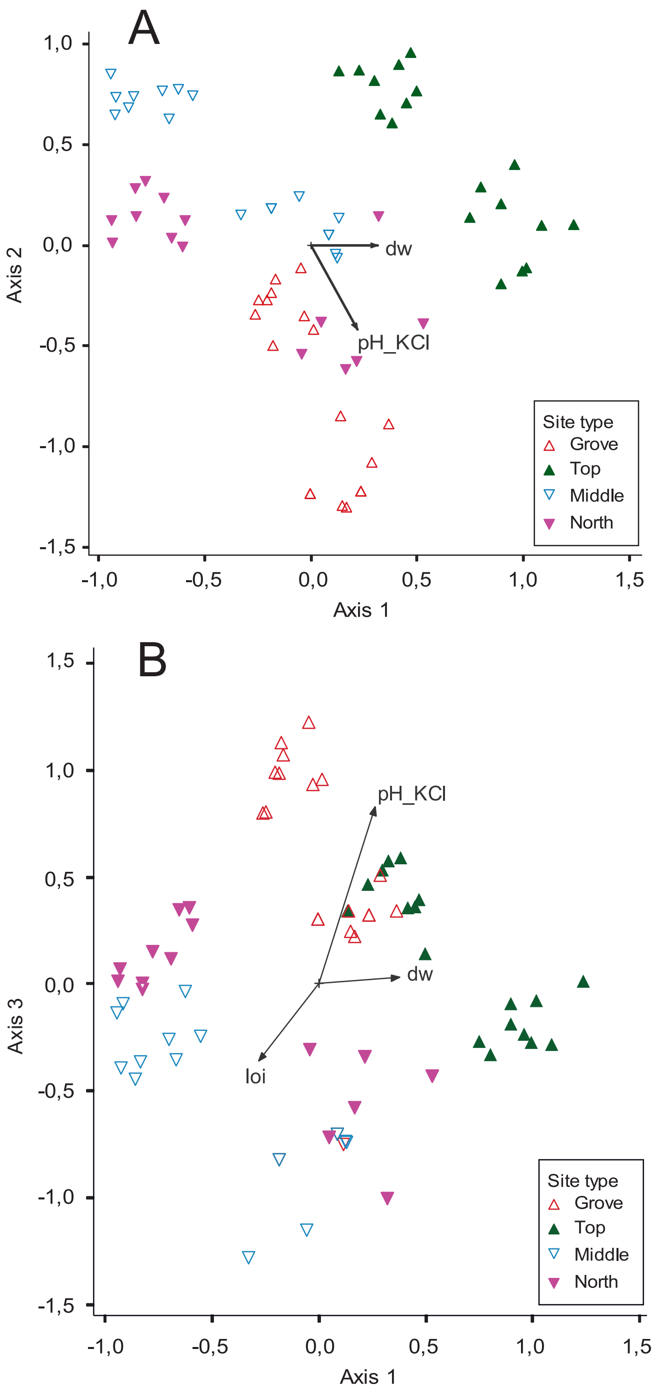

Figure 5. The joint plot of NMDS ordination for plant species composition. All replicate plots of each study site with vegetation surveys done in late May, July and early September in 2004 and 2005. The vectors of environmental variables with strongest correlation to ordination axes ($r > |0.5|$) are shown. The upper panel (**a**) includes axis 1 and axis 2 and the lower panel (**b**) includes axis 1 and axis 3.

Grove treatments now being the most distinct (Fig. 5). The vectors of the two environmental variables, soil dry weight (dw) and soil pH (pH_{KCl}), were positively correlated to axis 1 and axis 3 (r = 0.50 and 0.74, respectively) whereas soil pH was additionally negatively correlated with axis 2 (r = -0.58). This observation indicates that these environmental variables did not form a readily observable gradient as in the enzyme activity ordination.

A three-dimensional solution was also achieved with NMDS ordination including monthly means of within-site replicate plots of plant composition data (final value of the stress function = 5.09). Successional vectors joining monthly samples of experimental treatments showed parallel directional changes in all four areas (Fig. 6). The 20 most abundant plant species were widely scattered around Grove, Middle and North samples on the ordination plots (Fig. 6). There is a tendency for species of more nutrient-rich and moist environments (e.g. *Cirsium arvense* and *Filipendula ulmaria*) to group close to Grove samples, but no strong relationships are evident. However, no species grouped close to Top samples, which probably reflects the sporadic vegetation due to harsh environmental conditions there.

The cluster analysis on the basis of enzyme activities was applied separately for the data for the years 2003 and 2005. The pattern was characteristic to each site at the onset of the study in 2003 and, with one exception, all the samples from different dates formed a site specific sub-cluster (Fig. 7). The reference forests, Middle + North and Grove + Top formed the main clusters. During the next year the activity patterns changed only slightly (data not shown), but they changed further in 2005 and a different picture was seen (Fig. 8). Site-specific groups were again observed, but the autumn samples from Alder reference forest were different (higher activities were generally observed) from the other forest samples. North + Grove formed a main cluster. Top was closer to this cluster, whereas Middle was most different from the other groups.

The relative enzyme activities per SOM between sites from 2003 to 2005 (Figs 7 and 8) changed and variation was observed for the reference forests. PME, chitinase, β-xylosidase and β-glucosidase activities decreased in Middle, β-xylosidase decreased in Grove and chitinase increased in Top from 2003 to 2005. Arylsulphatase, not included in the cluster analysis due to lacking data for 2005, displayed the highest activities calculated per SOM in Grove and very high activities were observed in September 2004 both in Grove and in Top sites (data not shown).

Discussion

Differences between sites

β-Sitosterol present in plant membranes indicates phytobiomass in soil and it has been shown that in early stages of decomposition it is degraded at about the same rate as bulk litter (Sinsabaugh et al. 1997). The strong correlation between β-sitosterol and SOM reflects the high proportion of relatively fresh litter in SOM in the study sites.

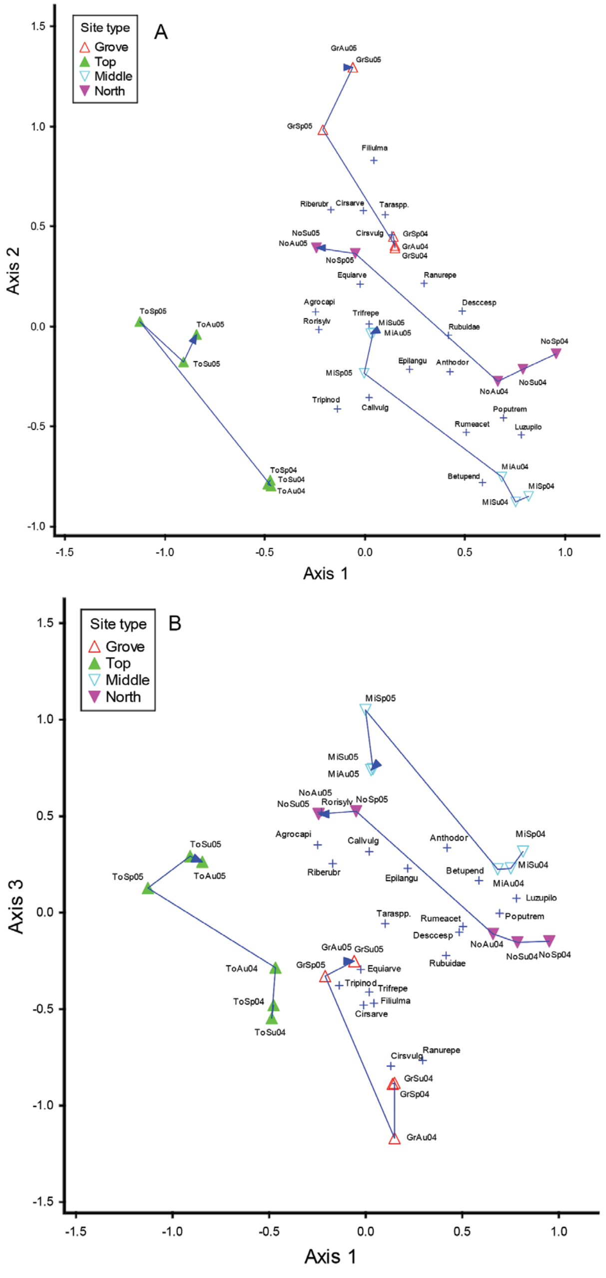

Figure 6. The NMDS plot showing temporal change in plant species composition. Successional vectors joining the monthly means of replicate surveys of each study site (i.e. experimental treatment) done in late May, July and early September in 2004 and 2005. The upper panel (**a**) includes axis 1 and axis 2 and the lower panel (**b**) includes axis 1 and axis 3. Point labels show two initials of the site, sampling season and year (e.g. GrSp04 = Grove Spring 2003). Other season abbreviations are: Su = summer and Au = Autumn. Average positions in the ordination space are depicted for the 20 commonest species according to vegetation surveys. Species abbreviations show four initials of the genus and species names, respectively (see Table S1).

Sample	PME	PDE	LeuAP	AlaAP	Chi	α-Glu	ß-Xyl	Cell	ß-Glu
North07	1.91	0.92	0.76	0.87	0.97	0.49	0.93	0.51	1.19
North09	1.96	0.92	0.76	0.87	**1.17**	0.50	0.97	0.55	1.12
North06	2.06	0.94	0.77	0.89	1.10	**0.54**	1.01	0.67	1.19
North08	*1.86*	*0.82*	0.80	0.92	0.90	**0.56**	0.90	0.50	*1.03*
Grove07	1.90	0.95	0.86	1.00	*0.70*	0.46	*0.73*	0.60	1.21
Middle06	1.97	*0.77*	*0.71*	*0.81*	0.95	0.40	0.89	*0.43*	1.14
Middle09	1.98	*0.71*	*0.70*	*0.83*	0.85	0.36	0.94	*0.38*	1.05
Middle08	*1.83*	*0.66*	*0.62*	*0.77*	0.94	0.34	0.85	*0.45*	1.10
Middle07	1.86	*0.56*	*0.57*	*0.68*	*0.70*	*0.21*	*0.75*	*0.29*	*0.92*
Alder08	2.18	*0.81*	0.93	1.04	1.08	0.26	**1.04**	**0.74**	**1.39**
Alder09	2.16	0.84	0.82	0.96	**1.15**	0.28	**1.10**	**0.72**	**1.30**
Alder07	**2.27**	0.84	0.87	0.98	**1.23**	0.36	**1.09**	**0.87**	**1.45**
Alder06	**2.19**	1.05	0.81	0.97	1.05	0.38	**1.19**	**1.00**	**1.56**
Spruce06	**2.28**	0.85	*0.69*	*0.81*	1.09	*0.22*	0.88	*0.42*	1.10
Spruce09	**2.28**	0.90	*0.72*	*0.77*	**1.24**	*0.21*	0.86	0.52	1.05
Spruce07	**2.33**	1.00	0.75	0.85	**1.36**	0.28	0.95	0.59	1.25
Spruce08	**2.39**	1.01	0.83	0.94	**1.29**	0.36	**1.02**	0.68	1.28
Grove08	*1.85*	**1.15**	0.99	**1.11**	1.06	**0.59**	0.89	0.71	**1.34**
Grove09	2.05	**1.11**	**1.08**	**1.20**	0.91	**0.75**	0.85	**0.75**	1.26
Grove06	2.14	**1.14**	**1.00**	**1.20**	1.14	**0.69**	**1.05**	**0.90**	**1.49**
Top06	*1.64*	1.05	**1.01**	**1.11**	*0.65*	*0.22*	*0.73*	0.61	*0.57*
Top08	*1.55*	**1.09**	**0.99**	**1.13**	*0.66*	*0.12*	*0.71*	0.45	*0.69*
Top07	*1.67*	**1.11**	**1.04**	1.10	*0.72*	**0.56**	*0.76*	0.59	*0.71*
Top09	1.87	**1.07**	**1.05**	**1.15**	*0.63*	0.54	*0.71*	*-0.03*	*0.78*

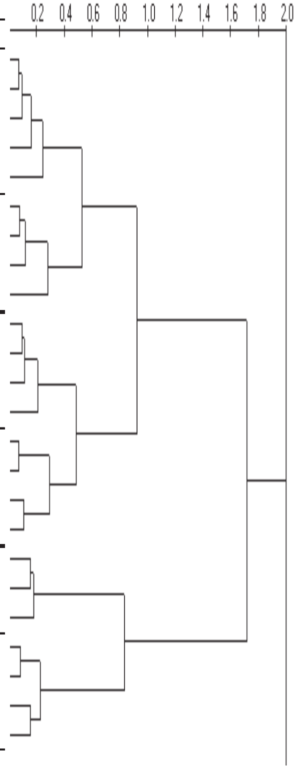

Figure 7. The dendrogram obtained by using means of enzyme activities per SOM in 2003. Triplicate samples of each site in June–September, lg transformed data (μmol MUF or AMC/g SOM in 3 h), standardised data, Gower's similarity coefficient and Ward's method. The original enzyme activity data is arranged according to the dendrogram to reveal differences between clusters. Sampling month (mm) is given for each sample. For each activity, the lower quartile is shown in *italics* and the upper quartile in **bold**.

There was also strong correlation between SOM and ergosterol, the indicator of fungal biomass, which shows fungal occurrence either as saprophytes but possibly also associated with new plant species developed on the constructed sites. Middle contained more β-sitosterol than North per SOM but due to the higher SOM content in Middle, the concentrations were reversed per dw.

Enzyme activity levels in soil per dw were clearly different between sites, true forests yielding the highest activities, followed by sites covered with old coniferous forest organic layer, of which Middle displayed higher activities than North, still lower activities in a site covered with alder forest soil with less organic matter and the lowest activities in hill top covered with mineral soil. The measurement of catabolic respiration patterns (Stevenson et al. 2004) reflect compositions of active microbiota in soil. Our results on soil enzyme activity patterns, affected by substrate availability and stabilisation of enzymes on soil surfaces in addition to the composition of microbiota,

Sample	PME	PDE	LeuAP	AlaAP	Chi	α-Glu	ß-Xyl	Cell	ß-Glu
Alder08	**2.14**	1.06	**1.08**	1.07	**1.39**	**0.51**	**1.27**	**1.05**	**1.61**
Alder09	**2.12**	1.03	**1.07**	**1.14**	**1.43**	**0.52**	**1.29**	**1.09**	**1.63**
Alder06	**2.11**	1.01	0.90	0.98	1.25	0.37	**1.21**	**0.94**	**1.45**
Alder07	2.04	*0.94*	0.88	0.94	1.23	0.14	**1.11**	**0.86**	1.40
Spruce06	**2.10**	1.08	0.87	*0.89*	**1.26**	0.24	0.99	0.75	1.28
Spruce07	**2.11**	1.10	*0.82*	*0.84*	**1.35**	0.32	*0.95*	0.69	1.24
Spruce09	2.08	*0.96*	0.89	*0.92*	**1.26**	0.15	*0.82*	0.51	1.09
Spruce08	**2.16**	1.11	1.05	1.12	**1.45**	0.22	1.02	0.67	1.31
Top06	1.86	**1.45**	**1.10**	**1.14**	1.01	0.21	1.11	0.77	1.09
Top09	*1.80*	**1.42**	**1.07**	1.07	*0.97*	0.18	1.10	*0.45*	*1.07*
Top07	1.90	**1.41**	1.02	1.10	1.01	*0.10*	1.09	*0.03*	*1.03*
Top08	*1.82*	**1.41**	**1.20**	**1.24**	1.07	*0.10*	**1.13**	0.73	*0.92*
North06	1.96	1.10	*0.81*	0.93	*0.95*	0.44	1.01	0.64	1.26
North07	1.95	1.19	*0.82*	0.97	1.03	0.36	1.07	0.73	1.28
North08	1.97	1.17	0.96	1.09	1.07	0.39	**1.12**	0.61	1.30
North09	1.90	1.08	1.01	1.01	1.10	**0.46**	1.04	0.68	1.37
Grove06	1.94	1.24	0.96	1.08	1.02	**0.56**	1.01	0.84	**1.44**
Grove09	1.96	**1.29**	1.00	**1.14**	1.17	**0.63**	1.06	0.84	**1.53**
Grove08	1.90	1.20	**1.10**	**1.23**	1.04	*0.14*	1.03	**0.93**	1.41
Grove07	1.90	**1.26**	0.97	**1.12**	1.01	*-0.97*	1.01	**0.86**	**1.46**
Middle06	*1.77*	*0.80*	*0.68*	*0.77*	*0.76*	*0.33*	*0.93*	*0.45*	*1.09*
Middle07	*1.78*	*0.79*	*0.66*	*0.74*	*0.77*	*0.08*	*0.85*	*0.37*	*1.07*
Middle08	*1.76*	*0.81*	0.85	0.93	*1.00*	**0.48**	*0.92*	*0.46*	*1.07*
Middle09	*1.53*	*0.79*	*0.57*	*0.68*	*0.65*	*0.12*	*0.70*	*0.11*	*0.92*

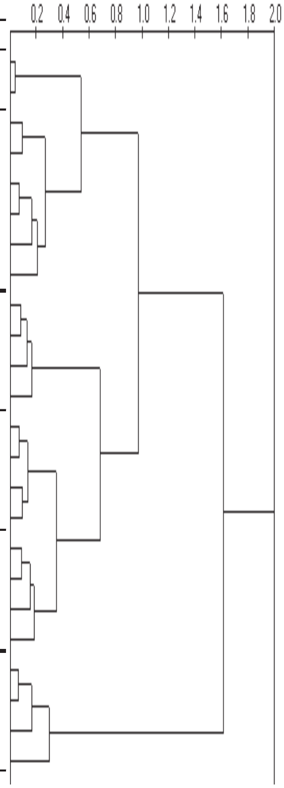

Figure 8. The dendrogram obtained by using means of enzyme activities per SOM in 2005. Explanations as in Fig. 7.

are in agreement with the observation by Stevenson et al. concerning the sensitive differentiation of soils with varying land use.

NMDS ordination revealed that the different study sites had characteristic enzyme activity and plant species compositional patterns. The enzyme activity patterns, normalized by calculation per SOM, were clearly dependent on pH, SOM content and mineral matter content (loi revealing organic matter and dw reflecting mineral contents). This observation is in accordance with the results of previous studies (Niemi et al. 2007, Niemi et al. 2008, Šturzová and Baldrian 2011, Wallenius et al. 2011). Surface soil moisture and temperature were less important, possibly due to seasonality simultaneously affecting all the sites and the fact that enzyme activity measurements were carried out under constant conditions and not at *in situ* moisture, pH and temperature. Furthermore, the actual enzyme activities in soil environment depend on substrate availability, whereas activity measurements were carried out without substrate limitation. The enzyme activity results reflect mainly the content of each active enzyme at the time of sampling, which is dependent on the composition of microbiota (Zimmermann et al. 2007). The vegetation compositional patterns were also characteristic for the experimental treatments, apparently illustrating differences in soil seed banks among the source areas from where surface soil was obtained and transferred to the treatment areas. This observation emphasizes the importance of soil seed bank in determining the plant species composition during the initial stages of vegetation succession that was already evident in the two years (2004–05) following the onset of the experiment (Supp. Figs S1–S3).

The study sites were clearly different in pH but each hill site exhibited a rather stable pH. The importance of pH for enzyme activity patterns plausibly reflected compositions of microbial consortia (Niemi and Vepsäläinen 2005). High SOM content tends to bring about low pH in coniferous soil due to organic acids, whereas high mineral and clay content tend to increase pH. The most important factors affecting enzyme activity patterns are interdependent.

In accordance with Niemi and Vepsäläinen (2005), cluster analysis revealed that relatively high mineral content and pH were associated with elevated PDE and aminopeptidase activities (Top and Grove). On the other hand, high SOM content and low pH were associated with high PME and chitinase activities (Spruce). High ergosterol content in Spruce plausibly indicates the importance of mycorrhizal fungi for these activities. Elevated activities of these enzymes and those responsible for cellulose and hemicellulose biodegradation, namely cellobiohydrolase, β-glucosidase and β-xylosidase, were evident even in Alder with relatively high pH. In general, many enzyme activities normalised by SOM content were the highest in true forests with mycorrhizal symbionts, diverse vegetation and high litter input. Our results conform with results on successional gradient of native prairie restoration showing that changes in microbial biomass were largely attributable to changes in SOM and N concentration together with root biomass (Allison et al. 2007).

Temporal change

One of the main aims was to study how enzyme activities persist in soil transferred from forest to the open hill. Activities calculated per dry soil (Fig. 2) were generally clearly lower in soils on the hill than in the forests at the onset of the study. This depended on the SOM content, which was much lower in the hill sites due to mixing with mineral soil. However, no decreases were observed during the monitoring. It is plausible that plant growth secured the rhizosphere effect and microbial activity even if the vegetation changed. The differences and changes within SOM were analysed in detail.

Both NMDS ordination and cluster analysis revealed a temporal successional change in enzyme activity patterns calculated per SOM between years. The hill top consisting primarily of mineral soil became more fertile, and in photographs taken in 2013, ten years after starting the experiment this change is also reflected by increasing cover of vegetation (Supp. Figs S1–S4). Unfortunately we don't have data on enzyme activities for this later time period, and thus quantitative comparisons with the early successional phase could not be performed. During the first three years of monitoring (2003-2005) after the onset of the experiment some enzyme activities were observed to increase also in Top soil SOM. The change in SOM quality might have been due to emerging vegetation and very slight increase in SOM content (14% but hardly statistically significant). Middle and North developed differently. North surface layer contained more mineral soil from the onset of the experiment, which kept it dryer and with higher pH, and also yielded lower sterol contents per dry soil. Its SOM contained the same level of ergosterol, indicating similar fungal biomass, and less β-sitosterol, indicating a less strong plant impact, than Middle. More dense grass (Poaceae), especially *Deschampsia flexuosa*, vegetation developed in Middle than in North (Supp. Table S1). However, enzyme activities increased in North, when compared with Middle, revealing different development in rhizosphere and impact on microbial activity. Dense grass cover reduces or even outcompetes many other low-growing plants which is detrimental to biodiversity, because the number of herbivorous insects and their associate species declines severely (e.g. Morris 2000, Pöyry et al. 2006). The relative change between North and Middle was mainly caused by increase in many enzyme activities in North rather than by decreases in Middle.

NMDS ordination also showed changes in plant species composition that occurred in all study areas towards the same direction during the first two years of monitoring that covered early phases of the vegetation succession. These changes clearly indicate the early phases of plant succession (Supp. Table S1, Figs S1–S3), following the establishment of plant species initially from the seed bank that was preserved in the transferred surface soil. Vegetation succession was fastest in Middle and North, whereas in both the moist depression (Grove) and the most exposed site (Top) change was slower based on the axis 1 of NMDS ordinations (no apparent differences in temporal change among sites on axes 2 and 3; see Figs 5 and 6). This pattern was against what we hypothesized. It may reflect a larger species pool being able to grow in more average environmental conditions of Middle and North sites than in more extreme conditions of Grove and Top sites. Therefore, various factors such as interspecific competition, antagonistic relationships and stochastic processes operating with more species can create faster and bigger changes.

The exact reason that would explain the parallel directional change across all experimental treatments remains unclear as none of the explanatory variables measured from the soil samples was correlated with the observed changes in plant composition, but one potential explanation is the increasing vegetation height caused by the same dominant species during early succession. Unfortunately, as with enzyme activities, we do not have data for plant occurrences for the period of ten years after the onset of the experiment (Fig. S4), and thus quantitative comparisons between the early phases of vegetation succession and the later time period were not possible. Grove site has developed to a true grove, but North and Middle sites still look like pastures after a decade.

Conclusions

A landfill site covered with forest soil top layer developed rapidly to urban green space. Soil enzyme activities increased markedly due to the forest soil cover, but remained lower than in the true forests. Soil enzyme patterns were characteristic to each site. They changed during a 3 year monitoring period reflecting differences in developing vegetation.

The value of integration of soil ecological knowledge with other successional patterns, such as changes in vegetation, in restoration management has been emphasised by several authors (Anderson 1995, Heneghan et al. 2008, Vauramo and Setälä 2010). Our study confirms the advisability of this approach. The transfer of forest organic surface soil to the mineral soil hill clearly increased soil biological activity for the three year duration of the monitoring. Microbial activity level followed the SOM content but the quality of the SOM affected the enzyme activity patterns. Vegetation increased rapidly in the sites covered with forest organic soil and even the establishment of mycorrhizal symbiosis is expected to be enhanced in covered areas (Lunt and Hedger 2003). We suggest that transferring the surface soil humus layer is a useful approach for ensuring the outcome of habitat restoration and complementary habitat creation especially in situations where the source soil areas would otherwise be lost.

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Supplementary material 1

Table S1

Authors: Maarit Niemi, Juha Pöyry, Ilse Heiskanen, Virva Uotinen, Marko Nieminen, Kirsti Erkomaa, Kaisa Wallenius

Data type: occurrence data

Explanation note: Vegetation data used in the ordination analyses.

Supplementary material 2

Figure S1

Authors: Maarit Niemi, Juha Pöyry, Ilse Heiskanen, Virva Uotinen, Marko Nieminen, Kirsti Erkomaa, Kaisa Wallenius

Data type: photograph

Explanation note: The studied sites at the onset of the study in June 2003: **a**) Top **b**) Grove **c**) Middle **d**) North **e**) Alder **f**) Spruce.

Supplementary material 3

Figure S2

Authors: Maarit Niemi, Juha Pöyry, Ilse Heiskanen, Virva Uotinen, Marko Nieminen, Kirsti Erkomaa, Kaisa Wallenius

Data type: photograph

Explanation note: The studied sites in August 2003: **a**) Top **b**) Grove **c**) Middle **d**) North.

Supplementary material 4

Figure S3

Authors: Maarit Niemi, Juha Pöyry, Ilse Heiskanen, Virva Uotinen, Marko Nieminen, Kirsti Erkomaa, Kaisa Wallenius

Data type: photograph

Explanation note: The studied **s**ites in August 2005: **a**) Top **b**) Grove **c**) Middle **d**) North.

Supplementary material 5

Figure S4

Authors: Maarit Niemi, Juha Pöyry, Ilse Heiskanen, Virva Uotinen, Marko Nieminen, Kirsti Erkomaa, Kaisa Wallenius

Data type: photograph

Explanation note: The studied **s**ites after a decade in June 2013: **a**) Top, **b**) Grove **c**) Middle **d**) North.

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Uncertainty in biodiversity science, policy and management: a conceptual overview

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Abstract

The protection of biodiversity is a complex societal, political and ultimately practical imperative of current global society. The imperative builds upon scientific knowledge on human dependence on the life-support systems of the Earth. This paper aims at introducing main types of uncertainty inherent in biodiversity science, policy and management, as an introduction to a companion paper summarizing practical experiences of scientists and scholars (Haila et al. 2014). Uncertainty is a cluster concept: the actual nature of uncertainty is inherently context-bound. We use semantic space as a conceptual device to identify key dimensions of uncertainty in the context of biodiversity protection; these relate to [i] data; [ii] proxies; [iii] concepts; [iv] policy and management; and [v] normative goals. Semantic space offers an analytic perspective for drawing critical distinctions between types of uncertainty, identifying fruitful resonances that help to cope with the uncertainties, and building up collaboration between different specialists to support mutual social learning.

Keywords

Uncertainty, biodiversity science, biodiversity management, biodiversity policy, semantic space, dimensions of uncertainty, social learning, learning cycle

Introduction

Uncertainty is an essential ingredient of science, manifested in all phases of conducting research, drawing conclusions, and putting the conclusions into societal practice (Funtowicz and Ravetz 1990). However, in biodiversity science uncertainty has been addressed mainly with a narrow focus on the precision of various numerical estimates. The Millennium Ecosystem Assessment (2005), for example, was an effort to come to grips with the global dimension of the loss of biodiversity. Somewhat paradoxically, though, the Millennium Assessment was made in such a generalized mood that uncertainty did not find a natural niche in the results. In Chapter 4, "Biodiversity", the report takes up uncertainty only in connection with estimates of species numbers. A similar lack of specificity is detectable in the important reviews published by *Nature* on the eve of the Rio+20 conference in early summer 2012 (Barnosky et al. 2012; Cardinale et al. 2012; Ehrlich et al. 2012). Every one of them mentions uncertainty as an important theme but in none of them is uncertainty specified except loosely in a contrast space between reliable knowledge vs. lack of knowledge.

This is insufficient. Biodiversity is such a multidimensional and complex issue that different sorts of uncertainties are inherent in many dimensions of the ecosystems themselves and of biodiversity research. Specifications are needed as to what, precisely, is uncertain, what is the reason for the uncertainty, and whether the uncertainty matters. Further below, we use the notion of semantic space to explore key aspects of uncertainty in the context of biodiversity science, policy and management (see also Haila et al. 2014).

Biodiversity is a knowledge intensive concept. The concept was conceived by biologists worried about the consequences of accelerating human-induced changes in the ecological conditions of the Earth; the story is well known (Wilson and Peter 1988; Takacs 1996; Haila 2012). Conservation biology originated as a new biological sub-discipline at the same time (Soulé 1985). The founding ethos is well-taken: there is no way to come to grips with the human ecological predicament without adequate knowledge basis. But this statement, of course, implies that the uncertainties of knowledge concerning biodiversity have to be analyzed seriously. The goal of policy relevance brings into the picture yet other dimensions of uncertainty that pertain to social and political implications of the knowledge produced.

Let us add a clarification on this point. There is nothing uncertain in the assertion that biological diversity is a critical feature of the life-support system of the Earth, to use Eugene P. Odum's phrase (Odum 1989). Neither is there any uncertainty on a general level that the increasing human encroachment on the Earth's ecosystems causes deterioration of biodiversity. But these general statements do not mean that any claim or prescription concerning biodiversity is valid. First of all, there is a discrepancy between the "bigness" of the issue and the level of detail needed to address it (Haila 2004). Another major dimension concerns the feasibility of policy recommendations that are offered to the society. As political scientist Giandomenico Majone stresses, the (in)feasibility of one or another policy goal is not a natural given. Drawing conclusions on what is feasible and what is not is a part of the research setting. In Majone's view, feasibility analysis aims at changing the conditions of feasibility (Majone 1989). There are no shortcuts: promoting a simplistic solution in a situation riddled with uncertainties may lead to unanticipated and counterproductive consequences (see also Mitchell 2009).

There is a deep ambiguity in the human ecological predicament: whatever we do we change the environment, and we cannot avoid also detrimental effects – in fact, we often do not know precisely, what is detrimental. Furthermore, what is detrimental in one set of conditions may be favourable in another set of conditions. Variability in mechanisms that maintain soil productivity provides examples: what works at one place may be positively harmful somewhere else. In other words, the relationship between generality and precision needs concern. The situation resembles that encountered in debates about climate policy (Pielke 2007, Hulme 2009), but it is also different in interesting ways. We will get back to this point below.

To chart the whole field, two round-table discussions were held at Helmholtz Centre for Environmental Research, UFZ, Leipzig, in autumn 2011 under the title *Exploring uncertainties in biodiversity science, policy and management.* The perspective was pragmatic: the aim was to produce an overview from a bottom-up perspective on how natural and social scientists involved in biodiversity research have come across uncertainty in their working practices and how they have coped with it. We dubbed the domain of the workshop *biodiversity praxis* (Haila et al. 2014).

The work of Silvio Funtowicz and Jerry Ravetz (1990, 1991) offered us basic inspiration while we made preparations for the workshops. A particularly useful part of their work is the distinction they draw between quantitative and qualitative aspects of uncertainty. They specify what kind of categories an assessment of the qualitative uncertainty of scientific information should take into account: "(F)or a general understanding, we have to distinguish among the technical, methodological, and epistemological levels of uncertainty; these correspond to inexactness, unreliability and "bordering on ignorance," respectively." (Funtowicz and Ravetz 1991).

For assessing different types of uncertainties in scientific knowledge Funtowicz and Ravetz (1990) developed a scheme that is known by the acronym NUSAP. This figured at the background of our project, and we were greatly helped by later systematic applications (van der Sluijs et al. 2005, 2008) but we refrained from organizing the discussion according to the scheme as we wanted to explore a more open-ended agenda.

In the paper that follows this introductory essay we present the materials of the first workshop, held on 3–4 November 2011. Most of the 18 participants were working within the auspices of the EU 7th framework project SCALES (*Securing the Conservation of Biodiversity across Administrative Levels and Spatial, Temporal and Administrative Scales*) (Henle et al. 2010), but the group was complemented with a few staff-members of the UFZ who brought into the discussion their specialized perspectives. The discussions were recorded and transcribed. The transcriptions were used to reconstruct main themes that came up during the workshop.

The SCALES project offered a promising framework for the endeavour. It is broad and ambitious enough to provide a good overview of themes for which uncertainty matters. Furthermore, the project addresses explicitly uncertainty in several research tasks. Another workshop was organized on 7–8 December. The compilation of papers collected in this special section of *Nature Conservation* includes, in addition to this introductory text, a thematic overview of the November workshop (Haila et al. 2014) and specific "standpoint" essays that were invited from the participants of both workshops. Magnusson (2014) discusses the uncertainties one has to deal with in the planning of in-situ monitoring programs from study design to data collection and analysis to management of programs and to linkages with stakeholders. He concludes that to be successful monitoring programs need to take these uncertainties into account already at the early conceptual stage. Pe'er et al. (2014) take up another attitude to uncertainty and elaborate upon the possibility that uncertainty could be embraced. They spell out several ways in which the effort exclusively to reduce uncertainty may be counterproductive, and demonstrate that well articulated uncertainty can have positive effects in knowledge production.

On uncertainty: Pre-analytic starting points

Uncertainty needs not be formally "defined". It is best regarded as a cluster concept, which gets different specific shapes in different contexts. In general terms, uncertainty pertains to the cognitive relationship of human agents to choices on what they do or prepare to do in a particular situation at a particular time. The inherent complexity of real world systems humans are faced with is a major source of uncertainty. In this broad sense uncertainty has a pervasive presence in all practical decisions people make both in daily routines and when getting prepared for the future either individually or as agents in institutions (Tversky and Kahneman 1974; Kahneman and Tversky 2000).

Our perspective implies that uncertainty has an ambiguous character. Uncertainty comes in many different guises, and in any particular situation it may be difficult to pin down what, specifically, is uncertain. Economists, in particular, have been aware of this ambiguous nature of uncertainty – quite understandably, in fact, as they have been interested in human economic actions oriented toward future that is never known in advance (Knight 1921, Keynes 1937, Shackle 1955). The extent to which the future is predictable is a key issue in this regard. A distinction needs to be drawn between measurable and unmeasurable aspects of uncertainty about future events; Knight (1921) drew the distinction as follows: "(i)t will appear that a measurable uncertainty, or "risk" proper, as we shall use the term, is so far different from an unmeasurable one that it is in effect not an uncertainty at all."

The dream of measurability of future events was given a formal supporting argument by French mathematician Pierre Laplace in the 18^{th} century. He claimed that a demon with perfect knowledge of the world would be able to predict the future with perfect accuracy. However, the Laplacean dream has been put to rest by the research on nonlinear dynamics that had its origin in the work of Henri Poincaré in the late 19^{th} century. Since then, both formal-mathematical and conceptual studies of complexity, non-linearity and chaos have made considerable progress. With the help of the huge increase in computing power during the last few decades, a lot has been learned about qualitatively specifiable features of uncertainty in different types of chaotic systems (e.g., Ekeland 2006; Smith 2007).

The general lesson is: uncertainty does not mean that anything can happen anywhere anytime. In other words, the set of possible ways a particular system can change is bounded, but the tightness of the bounds is relaxed with increasing time (Lorenz 1993). In addition, the studies on complexity and chaos bring forth more specific messages. First of all, the structure of the system gives hints about the shape of its possible future change. Physicist Leo Smith (2007) specifies three aspects of knowledge that have a decisive influence on our ability to assess the future trajectories of any system of interest: first, the current state of the system; second, the identities and values of critical parameters; and third, the adequacy of the structure of the model we have of the system.

In practical terms, the model adopted of the system of interest is critical. Philosopher Sandra Mitchell (2009) promotes an epistemological strategy she calls integrative pluralism to cope with complex research problems. "(T)he history, the context, and the dynamics of systems play leading roles" in the strategy. Her points are remarkably similar to the three points of Smith (2007). We can conclude that there is a direct link between the type of model adopted and the semantic space of uncertainty affiliated with that model.

It is useful to think of a semantic space in terms of dimensions, as always is the case with abstract spaces. The dimensions of a semantic space can be identified using the idea of a contrast space as a means. Alan Garfinkel (1981) articulated the idea using physical phase space as an analogy. A contrast space is defined by axes that stand for alternative perspectives for making the phenomenon of interest understandable. The overall view of the phenomenon "moves" in the abstract space depending on assumptions concerning these alternatives; this application of the idea draws upon Dyke (1988, 1993), see also Haila (1998).

In accordance with the contrast space perspective, we adopted a few distinctions that were used as a background for the workshops. These were regarded pretty much as self-evident in the discussion. The first such distinction was between uncertainty and risk. Economists have been well aware of this contrast since the 1920s, as we noted above. The second distinction was between epistemic uncertainty pertaining to knowledge and stochastic uncertainty pertaining to ontology of the world, customarily drawn in the context of sensitivity analysis (e.g., Saltelli et al. 2008). The third relevant distinction stems from the criteria of making decisions about uncertainty at a cut-point, as is routinely done in scientific practice, by drawing a distinction between type I (rejecting a true null hypothesis) and type II (accepting a false null hypothesis) error. This distinction has been amended by naming an error of third type that brings up qualitative aspects of uncertainty: type III error is made if the question asked is incorrect or irrelevant (e.g., Dunn 2001; Kriebel et al. 2001).

The three distinctions presented above correspond to three dimensions of the semantic space of uncertainty. The dimensions are relatively independent of one another.

It is, for instance, perfectly legitimate to ponder upon type I vs type II error irrespective of whether the uncertainty assessed is epistemic or ontological. When organizing the workshops, we were mainly interested in substance-specific dimensions of uncertainty in biodiversity research. We present a preliminary model of the semantic space in the final section of this paper.

On the specificity of biodiversity research

The general features of unpredictability presented above are pertinent as regards the ecological realm where conditions are changing all the time in unpredictable ways. In its youth in the late 19th century, the science of ecology viewed nature through a "balance of nature" metaphor, but it was soon realized that ecological conditions are in a continuous change. Alfred Lotka's classic *Elements of Physical Biology* (Lotka 1924) was a landmark in this regard. Incidentally, Lotka was greatly inspired by Poincaré's work. More recently, this view has broken through in thinking about human relationships with the rest of nature (e.g., Botkin 1990).

To approach the semantic space of uncertainty of biodiversity praxis, a comparison between biodiversity and climate change is instructive. There is a clear difference between these fields stemming from the different nature of the medium: the Earth's atmosphere is a unified geophysical system whereas the biosphere is divisible into different sections or subsystems, geographically, taxonomically and ecologically. Furthermore, the divisions are descriptively complex (Wimsatt 1974), that is, when alternative criteria are used to carve a particular section of biodiversity into components, different kinds of patterns result.

A practical comparison clarifies the example. When compiling background data on climate change, it is possible to take estimates of green-house gas discharges of single countries such as, say, China, Canada and Guatemala, and extrapolate the effect of each of them to the global atmospheric balance. In the case of biodiversity, no comparable extrapolation is possible. Also the social consequences of biodiversity loss are much more unequivocal than of climate change. The question of contextuality is raised: symptoms, probable consequences, and policy implications of threats vary in a much more context-specific fashion in biodiversity policy than in climate policy (not denying that socio-economic differences across countries are relevant in climate policy, too).

The driving motivation of the workshops at the UFZ was the need to specify types of uncertainty in biodiversity praxis. There is no single way to reach this goal. We have to proceed along several mutually complementary lines. A good start is to ask the three simple clarifying questions we referred to in the opening section of this paper: What, precisely, is uncertain? Why, specifically, is this thing uncertain? And finally, does the uncertainty matter, and if it does, in which sense? Every ecologist with field-work experience can come up with examples of such a chain of questions, pertaining to a specific research project, for instance, the taxonomic composition of the samples collected, or the correspondence between the samples and the populations sampled, and so on (Magnusson 2014).

However, such a purely empirical specification of uncertainty covers only one theme at a time. Generalizable concepts are needed. More interesting distinctions can be drawn by utilizing a theory of conceptual spaces developed by cognitive scientist Peter Gärdenfors (2004). In cognition, a "what" is a representation. The scheme of Gärdenfors builds upon a three-partite distinction between different types of representations that make up conceptual spaces. His terms for these types are 'subconceptual', 'conceptual' and 'symbolic'. The original work includes polemics against rival views within the cognitive science but we can use the scheme without going into these debates.

Gärdenfors demonstrates the differences between the three types of representation using as an example a jungle where people try to find their way. The first form, 'subconceptual' representation consists of what they come across and record, often without articulation: "dynamic interactions between people and their environment" (p. 34). The second, 'conceptual' representation gives order to what they record, using abstract categories; in the example: "representing traveling information in a spatial form" (p. 34). The third, 'symbolic' representation is used when the road is marked with name-tags that will be recognized and interpreted in a consistent way by the people involved, "it is also required that there is common knowledge of what places the names refer to" (p. 35).

The three types of representation can be affiliated with three types of uncertainty. Uncertainty on the subconceptual level is about whether observations are recorded properly. The conceptual level relates to whether the spatial representation is usable. The symbolic level relates to the consistency of the shared knowledge inscribed in the collection of name-tags. These distinctions are applicable to biodiversity science in a straightforward fashion: subconceptual is about methods used in collecting data, conceptual is about patterns detected in the data, and symbolic is about the credibility and social relevance of the conclusions.

To make the analogy more concrete, let's note that Gärdenfors' distinctions have a clear affiliation with the standards adopted to mitigate different types of errors in empirical reasoning. Type I and type II errors correspond to the conceptual level. The decision made as to the type of error that is of main concern has a major influence on how the resulting pattern may be used in further research or in management. Statistical tests aiming at avoiding type II error (assuming no effect while there actually is an effect) customarily accept 20% error rate as a standard, but this may be too strict in the case of useful rules of thumb that can be used in management, for instance (Kriebel et al. 2001). Type III error, on the other hand, relates to the symbolic dimension. The conceptual edifice constructed on the basis of research may not correspond at all to the question that is of concern (Henle 1995; Haila 2004; Henle et al. in press).

We use the analogy between cognitive types of representation outlined by Gärdenfors and dimensions of uncertainty when constructing a preliminary model of the semantic space of uncertainty in the final section.

Further clarification of the nature of uncertainty

We referred above to economists as pioneers in thinking explicitly about the implications of the unpredictability of future in the social domain. Their thinking about uncertainty has advanced a lot since the groundlaying work of Knight and Keynes almost a century ago and offers some further lessons.

In particular, the view on the nature of risks in the markets has undergone great changes in the last half a century or so. Journalist Justin Fox (2009) who is well informed in recent economic history tells the story by tracking the development in the views of academics in economics and finance up to the first decade of the 21st century. Briefly put, there have been two main issues that dominate the story: first, the rationality (or not) of the markets, and second, the possibility (or impossibility) to beat the markets by a clever investment strategy. One of the cornerstones in the discussion has been the view, generally held since the mid-20th century, that variation in market values follows random walk, at least in the short run. It is consistent with the rational markets hypothesis through a variant of the law of large numbers: given enough traders, all discrepancies in market valuation of different assets supposedly even out – almost in real time, given efficient enough investment tools. This argument is in line with the view promulgated by free markets champions such as Frederick von Hayek and Milton Freedman that the markets constitute the best possible means to handle economic information. As Fox (2009) shows, models used to analyze variation in market values have become incredibly sophisticated in the course of the last few decades.

The efficient markets hypothesis makes the distinction between risk and uncertainty all but vanish. In the domain of random walk, there are no qualitative distinctions between types of uncertainties. Everything is akin to quantifiable risk and can be taken into account in advance, given good enough models.

However, the economic life in the last three decades has not agreed with these assumptions. The recessions of 1987 and 1998 and the dot.com bubble in the early 2000s, not to speak of the latest crisis that the world plunged into in 2008, contradict the rational markets hypothesis and the models built upon that hypothesis. In other words, parallel to the development in thinking about the markets, the nature of radical systemic uncertainty inherent in the markets has been clarified. There is an element of ontological uncertainty in this setting: new forms of financial assets change the behaviour of market actors, which changes the behaviour of the markets in turn. In fact, Daniel Kahneman and Amos Tversky pointed out this possibility already decades ago (see the essays in Kahneman and Tversky 2000).

There is another, even more important implication of the change in thinking about the economic life that is breaking through the established orthodoxy: an emphasis on contextuality. Context-specificity of human reasoning itself is the starting point of Silva Marzetti Dall'Aste Brandolini and Roberto Scazzieri (2011) in their exploration of what they call "fundamental uncertainty". The classical work of John

Maynard Keynes on probability (*Treatise on Probability*) is at the background of their work. In several ways, their approach is remarkably similar to the one we adopted at the Leipzig workshops.

If uncertainty is inherently contextual, making sense of uncertainty in specific situations requires that we take into account several aspects of cognitive work and social reality. On the cognitive side, a good starting point is offered by the work of Peter Gärdenfors (2004) we referred to above. To clarify social and political aspects of the setting, problem framing is a useful methodological device. Framing means defining the scope or focus of the problem on the one hand, and the context in which the problem is perceived on the other hand (Fischer 1995, 2003; Schön and Rein 1994; Hajer and Laws 2006). As Schön and Rein (1994) argue, many intractable controversies about the environment, for instance, follow from the fact that different people frame the problems in different ways (see also Henle et al. 2013a). The idea of framing draws upon the view that social problems are defined discursively, as a result of contestations and struggles among different actors as regards the significance of the problems. An important aspect is disagreement concerning types of warrants that support different views of the problems: what kind of evidence is accepted as sufficient and valid (Majone 1989, Chandler et al. 1995).

Hence, an appropriate framing of problems includes an assessment of factors that back arguments concerning the nature of the problem, one way or another. Fischer (1995) introduced a useful scheme consisting of four potential types of warrants that can be used to argue for a case. Fisher's categories are primarily about the nature of knowledge and public acceptability. He dubbs the most concrete level "type and quality of specialist knowledge"; it is self-explanatory. The second one is "technical and management expertise" which takes up the availability of the necessary practical skills. The third level is "societal vindication or public consent" which broadens the societal sphere considered to include public participation, stakeholder opinions and so on. The fourth level is "ideological acceptability" which addresses the question whether what is demanded is concordant with shared societal goal-settings.

Fisher's scheme offers a good starting point to elaborate upon types of uncertainty related to specific issues of biodiversity protection. As an example, consider managing human wildlife conflicts (Klenke et al. 2013). Elements of Fisher's first level of warrants are provided by ecological analyses of the diet, behaviour and distribution of wildlife and contested resources. Elements of the second level are about management skills in terms of techniques to deter wildlife, to analyse management effects on wildlife viability, and funds to compensate for loss caused by wildlife. Elements of the third level are about getting landowners and other users of the area to consent with the aims and rules of wildlife protection. The fourth, most general level comprises views on the general acceptability of biodiversity protection as a societal ethical imperative.

We present a suggestion on how the schemes of Gärdenfors and Fischer fit together in Figure 1.

	Ideological acceptability
	Societal vindication, public consent
Symbolic level	
	Technical and management expertise
Conceptual level	
	Specialist knowledge: type and quality
Preconceptual level	

Figure 1. A scheme depicting the correspondence between levels of cognitive representation (Gärdenfors 2004; on the left) , and types of warrants of claims-making (Fischer 1995; on the right), from more concrete (below) to more abstract (above).

Toward collective collaborative assessment

Nobel economist Wassily Leontief (1971) expressed his view on the relationship of theoretical and empirical research in economics as follows:

"True advance can be achieved only through an iterative process in which improved theoretical formulation raises new empirical questions and the answers to these questions, in their turn, lead to new theoretical insights. The "givens" today become the "unknowns" that will have to be explained tomorrow. … An example of a healthy balance between theoretical and empirical analysis and of the readiness of professional economists to cooperate with experts in the neighbouring disciplines is offered by agricultural economics as it developed in this country over the last fifty years. … Close collaboration with agronomists provides agricultural economists with direct access to information of a technological kind. When they speak of crop rotation, fertilizers, or alternative harvesting techniques, they usually know, sometimes from personal experience, what they are talking about. … While centering their interest on only one part of the economic system, agricultural economists demonstrated the effectiveness of a systematic combination of theoretical approach with detailed factual analysis."

Leontief's passage is a clarion call to an integrative knowledge strategy. The spirit is identical with our view on the challenge that biodiversity praxis is facing. But we want to get further than only note the similarity. The next step to take is to identify main dimensions of specialized work that need to be integrated together in biodiversity praxis. In the preceding sections we took up two conceptual schemes that can be used to this end: the layers of cognitive space presented by Peter Gärdenfors, and the layers of social and political warrants of claims-making specified by Frank Fischer (see Fig. 1). When preparing the November workshop, we developed with the help of these devices a scheme of main dimensions of the semantic space of uncertainty in biodiversity praxis, using our previous experience on biodiversity research as an additional resource; this scheme is presented in Figure 2.

It seems natural to order the dimensions from more concrete to more abstract. In the beginning, there is the *data*, and issues concerning representativeness, methodological consistency, and so on: the "preconceptual" level in the scheme of Gärdenfors. Primary data have to be compressed so they give relevant information for the issue at hand. *Proxy* (or *indicator*) is a shorthand for this. Proxy is a representation, which raises the question of adequacy: does it reliably stand for the phenomenon of interest? A whole range of proxies have been used in biodiversity research, from very general ones, such as species number and habitat area, to very specific ones, such as the presence of indicator or "umbrella" species. There is a rich discussion on the relative merits of different proxies (Pereira et al. 2013, Henle et al. 2013b). A proxy basically corresponds to the "conceptual" level of Gärdenfors.

But the credibility of a particular proxy does not depend on the empirical background alone, as important as this is: background *concepts* enter the picture. A workable proxy requires conceptual support. The situation is utterly familiar in biodiversity research, as it already was in the early stages of exploratory research on species–area and species–abundance -patterns from the early 20th century on. This is the "symbolic" dimension of Gärdenfors: a question about the coherence of the way the understanding of the problem is phrased. Schematic models, such as the species–area curve, obtain the role of symbols in scientific work (Haila 1986).

The last two dimensions in Figure 2 move toward the societal sphere. We connect them primarily to Fischer's scheme. The fourth dimension depicted in Figure 2 represents a conglomerate of factors pertaining to societal decision-making: assessing the situation, setting targets, formulating policies for reaching the targets, and implementing the policies into practical management. This is, of course, a huge and complex conglomerate, but to keep the idea of the semantic space of uncertainty transparent, we collapse the whole into one dimension in this context. As it stands, it covers relatively well the third level of Fischer's scheme: "societal vindication or public consent". As the fifth dimension we depict the normative background, which corresponds to Fischer's "ideological acceptability".

The scheme in Figure 2 turned out to be useful as a preliminary structure for the discussion in the November workshop. The companion paper (Haila et al. 2014) gives additional and detailed substance to the idea. In addition, we want to make a couple of further points drawing upon Figures 1 and 2.

First of all, there are interactions between the axes of the semantic space presented in Figure 2, of course, but the point of the figure is to offer an analytic perspective for drawing interesting distinctions. The "cluster concept" nature of uncertainty implies that it is impossible to pool all important aspects together in any case; Andy Stirling (2006) makes a similar point in an analysis of the potential role of public participation in assessing complex issues. Our preliminary assumption is that particularly interesting variants of uncertainty "reside" at the interstices of the dimensions where particular types of uncertainties are transformed into and mingled together with other types of uncertainties.

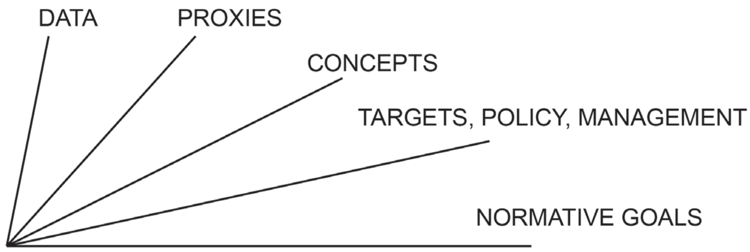

Figure 2. Main dimensions of the semantic space of uncertainty in biodiversity research.

As a means to specify further what is going on at interesting zones of transformation, we take up the idea of closure. As regards a knowledge-intensive issue, such as biodiversity protection, closure of knowledge and closure of policy go hand in hand; this view builds upon Chuck Dyke (1988) on knowledge, and Maarten Hajer (1995) on policy (see Haila 2008). The importance of closure is demonstrated by international goal-setting in biodiversity policy, which is burdened by too general targets that lack closure. For instance, the current target set by the European Union is to stop the deterioration of biodiversity by the year 2020. The previous target year, that was not reached, was 2010. The target of 2020 will not be reached either. The target does not include a clear idea about what its realization would actually mean for development trends, such as urban sprawl, increase in traffic volume and spread of traffic infrastructure, intensification of agriculture and forestry, and so on. In cynical moments, one tends to think that no lessons are drawn, instead, a formal agreement is reached to replace 2020 with 2030, and so on.

Another aspect of the model presented in Figure 2 is that science and policy are both integral elements in it, but the model also shows a way to keep them separated. There is a transition in the scheme in this regard between the first three and the last two dimensions, corresponding to a transition from the cognitive dynamics depicted by Gärdenfors to the social and political framing depicted by Fischer (see Fig. 1). The term "interface" often used in this context can be understood as a rich, multidimensional intersection between knowledge production and political action, allowing for joint construction of feasible management and policy goals (van den Hove 2007). The connections between knowledge and policy reach deep down in specific forms along the dimensions of the semantic space. Methodological decisions on collecting background data for monitoring, for instance, have political implications, but these are mediated by the selection of the proxy and its conceptual status and reliability (Magnusson 2014). On the other hand, uncertainty can be a trigger for acquiring increasingly relevant background knowledge as well as promoting discussion (Haila et al. 2014, Pe'er et al. 2014).

The normative backing is all-important, as was made clear in the workshop discussion (Haila et al. 2014). This relates to what we noted above on feasibility analysis, with reference to Majone (1989). Issues of feasibility versus infeasibility of particular policy schemes are raised primarily with respect to the last two dimensions, but this is not the whole story. Problems of technical feasibility reach, of course, all the way to the first dimension, for instance to the question: What sort of data is it possible to collect? Moral and ethical views and convictions of people also influence greatly what can and will be done. In other words, the situation has a shade of the "fundamental uncertainty" discussed by Silva Marzetti Dall'Aste Brandolini and Roberto Scazzieri (2011): what happens now, perhaps for purely contingent reasons, will influence what happens next.

As a final note: in the spirit of Leontief's recommendation cited above, a general consensus grew out of the discussions at the Leipzig workshops that successful and meaningful coping with uncertainty depends ultimately on a learning cycle that covers the whole recursive chain cycling through science–management–policy–science. We elaborate a learning cycle view in the concluding section of the joint workshop report Haila et al. (2014).

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RESEARCH ARTICLE

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Confronting and Coping with Uncertainty in Biodiversity Research and Praxis

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Abstract

This paper summarises discussions in a workshop entitled "exploring uncertainties in biodiversity science, policy and management". It draws together experiences gained by scientists and scholars when encountering and coping with different types of uncertainty in their work in the field of biodiversity protection. The discussion covers all main phases of scientific work: field work and data analysis; methodologies; setting goals for research projects, taking simultaneously into account the agency of scientists conducting the work; developing communication with policy-makers and society at large; and giving arguments for the societal relevance of the issues. The paper concludes with a plea for collaborative learning that would build upon close cooperation among specialists who have developed expertise in different fields in research, management and politics.

Keywords

Biodiversity science, biodiversity management, biodiversity policy, dimensions of uncertainty, governance of biodiversity, research practice, scientific agency, social deliberation, social learning, uncertainty

1. Introduction

Biodiversity is a multidimensional issue. When working with biodiversity, there are multiple sites of uncertainties involved at all stages from mundane steps of empirical field research to formulating political recommendations. However, uncertainty has usually been addressed from a narrow perspective (Haila and Henle 2014). "Exploring uncertainties in biodiversity science, policy and management" was the theme of a workshop held at the auspices of Helmholtz Centre for Environmental Research, UFZ, Leipzig, in November 2011. In this paper, we summarise issues that were taken up during the discussions.

The aim of the workshop was to establish a comprehensive agenda for assessing uncertainties in biodiversity praxis. We use the term 'biodiversity praxis' as a shorthand for all the activities supporting applied biodiversity conservation, including conducting research by collecting and analysing data, summarising and interpreting the results, drawing conclusions on conservation targets and formulating management guidelines and policy goals. All such tasks comprise decisions oriented toward the future. Formulating grounds for such decisions entails uncertainties.

We adopted a pragmatic focus: our goal was to produce an inventory of how natural and social scientists involved in biodiversity research have come across and coped with uncertainty in their working practice. The background of the workshop is described in more detail by Haila and Henle (2014) who also outline the pre-analytic starting points.

The workshop procedure was structured by short prepared presentations, most but not all of them with slides, invited from most of the participants with different background experience. The discussions were recorded and transcribed. This paper summarises main themes that were raised in the workshop, based on screening the transcripts (by YH) and a repeated editing process by the participants. As the paper is built on the points made by the participants during the workshop discussion, we use citations extracted and edited from the transcripts in the body of text. The speaker is indicated by his or her first and family names on the first occasions, and by the first name later on.

We adopted *semantic space* as a basic tool for drawing distinctions among specific types of uncertainties. A first step in analysing a semantic space is to define its dimensions (Haila and Henle 2014). This can be done by identifying practical and/or conceptual dimensions, which indicate the context of any specific type of uncertainty. We will get back to this point in the concluding section. In addition to the dimensions of the semantic space, two themes grew to serve as organising elements of the train of collective thought during the two-day discussion sessions:

[1] Of critical importance is the question asked and the type of data and model used to elaborate the case and identify what can potentially count as an answer. Our view of models as research tools is akin to the pragmatic perspective of Levins (1966) and Rosen (1991). A major issue relates to how the scope of the model is defined; Rosen (1991) used the term 'enclosure' to specify this step.

[2] The variety of practical roles that we, the participants, have had in our professional experience laid the ground for the discussions. This experience ranges from theoretical and empirical ecological and social science research, including the application of statistics and modelling, to science-policy dialogue, work in environmental administration, and hands-on biodiversity conservation.

In the following sections we take up main themes that were raised in the discussions of the workshops; the section titles are listed in Table 1. In the concluding section we give a suggestion on how to use the semantic space of uncertainties in biodiversity praxis as a tool that helps to specify what can be done to cope with uncertainty.

Table 1. The structure of the article.

1. Introduction
2. Starting Up
2.1 What is the question?
2.2 The basics of modelling
2.3 Assessing errors
2.4 Social-ecological models – a different species
3. Research to support biodiversity praxis
3.1 Scientific agency
3.2 To reduce, or to deal with uncertainty?
3.3 Multiple uncertainties in a well-elaborated case: The Norwegian Nature Index
3.4 Contingencies of adaptation
3.5 What about ecosystem services?
4. Social and political reception
4.1 Institutions and governance
4.2 Assessing governance success
4.3 Economic instruments
4.4 Precaution
4.5 The concept of biodiversity and its surrogates
5. Communication and societal relevance
5.1 Aiming at closures, albeit temporarily
5.2 Enhancing public discussion
5.3 Deliberation and social learning
6. Conclusions: collective effort with a division of labour

2. Starting Up

2.1 What is the question?

"Uncertainty becomes acute whenever we ask a question. If there is no question, there is no uncertainty. When we try to reduce uncertainty in one specific question we keep asking new questions, and more uncertainty will come out." (Joseph Tzanopoulos)

The question asked sets the stage. Alan Garfinkel used the notion of 'contrast space' to describe the set of alternatives among which the explanation has to be found for a specific problem. Contrast space makes explicit the context and precise sense of a research question (Garfinkel 1981; see Dyke 1988, 1993, Haila and Henle 2014). Answering a research question requires explanatory closure (Dyke 1988), and an appropriate contrast space indicates the boundaries of a closure.

With this requirement, we get to where strictly scientific questions end and other types of questions show up. The need to continuously ask new questions is an inherent part of the societal process of coping with changing conditions. New questions build upon existing knowledge. Closure, albeit a temporary one, is a method to bring together the elements deemed necessary for making sense of a question asked [see Sect. 5.1].

"One should try to narrow down the level of uncertainty by trying to ask a fairly concrete question. For me, this would mean in practical terms that if we ask new questions, we should not say older things are not important any more although that is often done in science. Nature conservation is perhaps sufficiently diverse in practice that we should retain a stronger memory." (Klaus Henle)

2.2 The basics of modelling

A basic epistemological strategy in empirical research is to explicate the context of the research question by constructing a model. The model delimits the research object by making visible the basic structure of the object being modelled so that necessary data can be collected, preferably experimentally although this is seldom feasible in field conditions, and calculations can be performed. A model abstracts and leaves out what is not considered essential (e.g., Levins 1966, Puccia and Levins 1985, Pielou 1977, Wimsatt 2007). For complex objects, such as biodiversity, decisions on what to include or exclude are seldom straightforward. When the decision based on the model is made, some uncertainty remains nevertheless. However, such uncertainties are often neglected when conducting research and communicating the results (e.g. Pe'er et al. 2013).

Several kinds of technical uncertainty are inherent in the modelling process and can be controlled to a certain extent by using systematic technical procedures. Regan et al. (2003) reviewed potential treatments of uncertainty in the case of population models.

Another type of uncertainty stems from deficient knowledge of the process under research, caused for instance by incomplete data sets.

"Systematic errors are measurement errors, and mainly caused by imperfect calibration of the measuring process that produces data. We can take into account random errors as standard deviations of our parameters. --- So, we may sometimes deal with a lack of accuracy, or poor quality of our data, but models are meant to work also with imprecise data." (Yiannis Matsinos)

The nature of the research problem sets specific requirements on data quality.

"Incomplete data could be particularly detrimental when we deal with spatial modelling on different scales. --- It is important to focus on the quantitative aspects of assessment in modelling, to see how particular types of uncertainty affect model outputs in different scenario ranges, and to determine the accuracy of predictions that the model allows." (Yiannis)

In addition, the modeller faces the dilemma that processes in nature may be inherently stochastic. Consequently, it is very difficult if not impossible to trace such inherent stochasticity and detach it from uncertainty stemming from inadequacy or lack of data. In real life, scientists have to cope with stochasticity because it is simply impossible to get enough data. Weather forecasts demonstrate this problem very concretely: The system is utterly sensitive to small differences in initial conditions, as the "butterfly effect" parable of Edward Lorenz demonstrates (Lorenz 1993). But we have to recognize that stochasticity does not equal chaos.

"Can we handle the difference between deterministic and stochastic components of a setting? Sometimes we don't know if something is stochastic because it is stochastic by nature, or only seems stochastic because we do not know enough. So for me this differentiation is superimposed on our lack of knowledge and our wish to assume that everything can be explained." (Guy Pe'er)

2.3 Assessing errors

The distinction between type I error (rejecting a true null hypothesis) and type II error (accepting a false null hypothesis) is familiar, but drawing the borders requires care. In particular, the decision as to which one to emphasise is consequential. Statistics provides technical criteria for evaluating the reliability of the decision, but this is strictly conditional upon the formulation of the null hypothesis and the nature of the data [as to type III error, see Sect. 5.1].

Assessing errors is particularly relevant in biodiversity research studies that attempt to give advice for management. A manager may adopt a "rule of thumb" that cannot be validated by a formal statistical test because it functions only 70% of the time, say, due to variation in environmental or societal conditions.

"The determinism vs stochasticity balance is shifted toward the stochastic side when we move to societal issues, but in ecology at least, some processes can be regarded as reasonably deterministic. --- The question is, where to best place this balance. If you do the study only yourself, fine. You do the analysis and you know where you put the balance. But others may continue the methodological procedure and ignore the simplifying assumptions made when placing the balance. In statistics, we can witness an increasing move towards the use of information theoretical decision criteria, such as Akaike's Information Criterion for selecting among competing models. While the authors who introduced these concepts to biodiversity research outlined underlying assumptions and warned against careless interpretation of results [Anderson et al. 1994], when there is a lack of fit, most scientists applying such approaches nowadays do not care. I have shown with an example [Henle 2005] that this may lead to complete misunderstanding of relevant processes, and even to wrong management decisions." (Klaus)

2.4 Social-ecological models – a different species

Approaches to modelling in the social sphere are distinctly different from those adopted in the natural sciences. The differences are basically due to historical contingency and context specificity of processes in the social realm, but also to the fact that humans, as research objects, belong to the "interactive kind" (Hacking 1999). Research procedures certainly can affect target organisms, for instance when they are collected using traps, but only humans read research reports and may react to the conclusions by modifying their behaviour.

A fruitful possibility is to use socio-economic models in biodiversity research primarily for understanding and communication, and to refrain from making concrete predictions. Basically, the heuristics allowing generalizations are context specific in the socio-economic sphere. Objects modelled in the social sphere are hardly ever thought of as representations of a background population that would constitute a natural domain for generalizations. Rather, socio-economic models can be viewed as analogues that allow qualified generalisations over cases of a similar type (Haila and Dyke 2006; Haila and Loeber 2009).

"In social-ecological modelling, we use process-based simulation models, which include ecological and socio-economic components and feedbacks. We often use very simple models, we call them toy models, which are not aimed really for prediction, but rather for understanding, and as a tool of thinking and communication [Schlüter et al. 2012a]. We do our work together within an interdisciplinary team that includes ecological economists and has recently been augmented with social geographers. Qualitative and quantitative information on different levels, on different scales, can be used to reduce the uncertainty in model parameters and in model structure [cf. pattern-oriented modelling, Grimm et al. 2005, Grimm and Railsback 2012]. We also use inverse modelling methods for this purpose [cf. Refsgaard et al. 2007]. Furthermore, these models can explicitly consider the attitude towards uncertainty, or adopt strategies to deal with uncertainty of the natural resource user [Quaas et al. 2007, Müller et al. 2011].” (Birgit Müller)

For dealing with practical issues of natural resource management and conservation, participatory modelling has gained importance in the last decade (for a review see Voinov and Bousquet 2010). Here different groups of stakeholders participate in the modelling process. Different goals and problem framings of the stakeholders can be considered and made explicit to the researchers and other stakeholders right from the beginning (see also Schlüter et al. 2012b). The identification and characterisation of all sources of uncertainty can be made jointly (cf. Refsgaard et al. 2007 for an overview on uncertainty in the environmental modelling process). The collaborative learning process thus enhances problem understanding, inclusion of relevant factors and acceptance of the model outcomes.

A further approach – management strategy evaluation – may turn out to be promising for research on conservation issues in the future (Bunnefeld et al. 2011, Milner-Gulland 2011). In a virtual world, management scenarios can be evaluated for their robustness to uncertainty. This approach comes from fisheries science and includes stakeholders in the model. Exemplarily, a policy maker can set a fishing quota and determine the appropriate level of monitoring of catches by the fishermen. In the real world, full information is never available on fish catch, but rather it depends on the monitoring effort, which is associated with different levels of costs. In the virtual world, one can vary the knowledge of the system, so that different monitoring scenarios can be compared in terms of their cost/benefit ratios. This approach is closely related to the virtual ecologist approach (Zurell et al. 2010).

3. Research to support biodiversity praxis

The practical purpose of research is to increase understanding and explanatory capacity concerning the phenomenon of interest and, thus, to support reasonable recommendations on what should be done. This is a pragmatic dimension of biodiversity praxis. However, there is no smooth linear transition from the realm of research to the realm of policy across what is often depicted as the ”science–policy interface.” Rather, the transition implies choices between several interpretative frameworks concerning what aspects of the results to emphasise and what significance to give to uncertainty (Haila and Henle 2014).

3.1 Scientific agency

Scientists have had a major role in identifying biodiversity loss as a major problem, ever since the foundational BioDiversity meeting held in Washington DC in 1985 (Wilson and Peter 1988). Scientists initiated the discussion and constructed the arguments. Hence, the nature and credibility of scientific agency counts. The challenge for scientists is not only to produce knowledge. In fact, as Sarewitz (2004) argues, arguments derived from science alone may make environmental controversies worse by hiding from sight value conflicts that need to be articulated in order that social and political assessment of the nature of the problems is possible.

Value systems and ideological positions influence attitudes of scientists toward developing strategies for promoting the social relevance of what they do (Apostolopoulou and Pantis 2009). It is therefore advisable to take a pragmatic perspective as regards value assessments (following, for instance, Simon 1981 and Majone 1989): given alternative possibilities for action, values give guidance as to which one to choose. Furthermore, previous experience matters for the stabilization and articulation of values in specific situations.

In science, the type of successful work conducted previously acts as a point of reference, without which one cannot explain anything (Russell 1979). Similar to all humans, scientists are biased to some extent by their experience. Also, science is a historically and culturally dependent activity that extends a particular vision of reality through networks of power (Latour 1987, Hacking 1999). The way a question is posed and an answer is sought for determines at least partially the set of answers that can be obtained (Russell 1979, Gould 1980, Latour 1999).

"Scientists don't use only logical arguments. In an interview, a scientist gave me three advices: first, love the birds; second, love the birds; and third, love the birds. As Funtowicz and Ravetz [1990] point out, we as scientists have our stakes, and we have to make clear that we have our stakes. We want people to appreciate biodiversity." (Felix Rauschmayer)

Scientists may adopt alternative roles when going public. As Roger Pielke (2007) has pointed out, one possible role is to act as a knowledge broker by collecting different perspectives and presenting a balanced overview. Alternatively, a scientist may be an advocate who has a clear position in a particular controversial situation. This is a legitimate role as well (Orr 2004). Another role is that of "pure researcher".

"It's fine to have value components in your arguments, but one needs to be conscious about them. Then you can partially separate, let's say, logical arguments and value systems – although never completely. --- What is perhaps even more fundamental for politicians or any other stakeholders who deal with scientists is that scientists are often living in a system of their own theories and values in a broader sense. And scientists tend to adhere to their systems of theories and values. And it's often very difficult for them to change them." (Klaus)

3.2 To reduce, or to deal with uncertainty?

One of the obligations of scientists is to acknowledge the uncertainty pertaining to the practical mundane detail of the research process. This is all the more important as research on biodiversity and related issues has grown explosively during the last couple of decades (Henle et al. 2012). Science has acquired good methods and traditions to increase knowledge. In addition, however, we should acknowledge that uncertainty has different roles depending on the case at hand and the role we adopt.

"Does uncertainty have a varying role depending on the role we adopt? Do we have a different concept of uncertainty when acting as a lobbyist or advocate, as a knowledge broker, or when we act as, let's say, pure modellers? When being a lobbyist for butterflies in Israel, I would probably be much more easy-handed with uncertainties regarding the results as long as I can make a point that would move a policy maker to do something for the butterflies. But when I'm modelling, I'm much more careful to fix the confidence level to, say 0.05 or 0.04. When I'm facilitating workshops as a scientist, then perhaps I might use uncertainty primarily as a means to facilitate discussion." (Guy)

Scenarios are built-up images of possible futures with varying assumptions as to what kind of decisions are made (Settele et al. 2012, Spangenberg et al. 2012). Thus, scenarios offer potential for charting uncertainties depending on variation in initial conditions. When projecting index values toward the future, it is customary to use relatively simple indices to compress data on complex phenomena (Schubert 1991, Dziock et al. 2006) and assess with models the potential effect of various factors on the values; GDP (Gross Domestic Product) and HDI (Human Development Index) are examples in the socio-economic realm. The Norwegian Nature Index is a good example in biodiversity research [see the next section].

"There are two things: we want to reduce uncertainty and we want to deal with it. To reduce uncertainty, predictions probably would be a useful tool. For me the big question is whether the goal of formulating precise predictions can actually be reached. I tend to believe that eventually entropy keeps increasing. If we cannot actually reduce uncertainty, and we have to deal with it, then predictions and scenarios may primarily help us to see what alternative futures may be in the coming. And then based on good scenarios you can actually build strategies and try to be proactive." (Joseph)

When scientific results are used for policy advice, uncertainties become multidimensional. This situation calls for what political scientist Giandomenico Majone (1989) called *feasibility analysis*: exploring the conditions of possibilities and impossibilities when striving for particular societal goals. However, in Majone's view, feasibility analysis includes an element of active intervention to change perceptions about what is possible and what is not. Properly specified uncertainty might actually help in this regard (Pe'er et al. 2014b).

3.3 Multiple uncertainties in a well-elaborated case: The Norwegian Nature Index

The Norwegian Nature Index (NNI) is a framework for integrated measurement of the state of Norwegian nature and its biodiversity, mandated by a government decision in 2005. The NNI is based on more than 300 individual indicators representing a wide range of species, populations, and indirect indicators of biodiversity (e.g. dead wood), covering nine major marine, freshwater and terrestrial ecosystems (Certain et al. 2011, Nybø et al. 2011, Nybø et al. 2012). For each indicator, values were assessed or estimated for various geographical entities (municipalities, counties, the whole country), for the years 1950, 1990, 2000, and 2010, as well as for a hypothetical reference state used as a basis for scaling all indicator values to the same scale from 0 (worst) to 1 (best). The reference state was generally supposed to represent rather intact ecosystems with minimal human impact, except for the mainly semi-natural ecosystems of "open lowlands".

The process of developing the NNI revealed different types of uncertainties, from the traditional issues of precision and accuracy of natural science data to the more fundamental issues of the meaning of biodiversity and interpretation of the concept of the reference state. The assessments of indicator values were based partly on actual data and modelling, partly on expert judgement, and often on a combination of both. For most indicators, available data were not statistically robust, due to, for instance, a low number of subjectively-selected sites. Hence, some form of expert judgement or 'model-based inference' (Yoccoz et al. 2001) was required in extrapolating from measured or observed data to years and sites where such data were lacking.

This type of uncertainty is within the scientific paradigm that most natural scientists are comfortable with. They have some data and knowledge about their indicator and the ecosystem(s) it is part of, and they can, with more or less confidence, say what the state of a particular indicator might be at different times and sites, even though actual observations are lacking.

It turns out, however, that individual experts vary considerably in their ability or willingness to use their expert knowledge to extrapolate indicator values beyond the set of observed values, and several have expressed concerns about the uncertainty involved in such extrapolations (Aslaksen et al. 2012a, Figari 2012). Paradoxically perhaps, it appears that experts used to working with the most accurate and precise population data were also the ones most reluctant to use their presumably excellent expert knowledge to extrapolate beyond their observations. Nevertheless, the uncertainties related to lack of accuracy, precision and spatial and temporal data coverage can be addressed by better sampling design and/or more samples in future data gathering.

The most immediate question of uncertainty in constructing the NNI appeared at the very beginning of the development process: How can a complex phenomenon, such as biodiversity, be captured by just a few indicators, and which indicators should be included to represent the state of nature and biodiversity? The core group in charge of the project decided early on to focus explicitly on biodiversity components as far as possible, i.e. by mainly using indicators based on some form of species population levels or indirect indicators with close association to species, and to avoid indicators representing direct drivers.

The actual selection of indicators was done by the invited experts in cooperation with the core group and was based on a specified set of criteria. The possible biases stemming from the selection process were then reduced by including more rather than fewer indicators and by weighing each indicator in such a way that each functional group defined had the same overall weight in the index (e.g., many primary producers were equivalent to a few decomposers). Some experts pointed to the uncertainty as to whether this resulted in an index sufficiently sensitive to key direct drivers and thereby producing an NNI relevant to the mandate.

In assigning values to the NNI, the experts were not just asked to assess values for their indicators for the present (2010) or previous years, but also to give their best assessments of indicator values for the future (2020), given current management policies for the relevant ecosystem (Aslaksen et al. 2012b). Such projections into the future raise new elements of uncertainty. Partly this may be seen as a statistical problem of forecasting based on time series of previous observations. However, only few indicators have sufficiently long time series of data with adequate precision to support credible forecasts.

In addition, most experts found it difficult to consider forecasting without worrying about some potential fundamental changes in management policies or ecosystem dynamics. A similar type of uncertainty may apply to assessment of indicator values in the somewhat distant past (e.g., 1950), where little credible supporting information may be available for most indicators. Such 'back-casting', as well as forecasting, would force the expert to address a more basic kind of uncertainty than the mere lack of precision or accuracy in the existing observations, namely the uncertainty of whether the fundamental dynamics of their ecosystems are preserved over time or not.

Perhaps the most challenging type of uncertainty about the NNI pertains to how the reference state is understood. It relates to more than a mere starting point for measurement. For each indicator, the experts must also link the concept of a reference state to the significance of observed changes in their indicators for the state of nature and biodiversity and decide on a scaling model for this relationship. Also, unless the various indicators relate to the same concept of a reference state (at least for the same major ecosystem), the values of the indicators cannot be compared or aggregated into one index.

For all major ecosystems except "open lowlands", a reference state based on intact natural ecosystems with minimal human impact was specified. However, various operational interpretations of such a reference state were allowed, reflecting quite different perceptions of the appropriate basis for comparisons against the current state among the experts. Some had fundamental objections to a reference state of 'pristine nature', others felt the overall objective of the NNI was better reflected by a reference state of sustainable management of ecosystems, whereas others simply found it impossible to decide on indicator values for a 'pristine' reference state. The conceptual uncertainty about the reference state continues to challenge the experts and their approach to the NNI.

3.4 Contingencies of adaptability

The public understanding of biodiversity may involve an unrealistic perception of a desirable static balance, but the components of biodiversity are evolving. Species survive in the long term only if they manage to adjust to environmental variation. Evolution is an existential game, and success means ability to stay in the game (Slobodkin and Rapoport 1974). This was Darwin's original insight. Yet this process has been embedded in historical contingency. The adaptability of different components of biodiversity depends on the time frame. Micro-organisms can adapt very quickly, as the continuous origin of resistant strains shows (Fisher et al. 2012), whereas elephants and polar bears are much less adaptable over the same time scales.

"In some directions in conservation biology, we try to incorporate evolutionary aspects as well. My question is: to which extent should we differentiate our biodiversity management in saying that we ignore such adaptive processes and the way species are able to incorporate them, or that we focus on them and say, well, it's not relevant what we have now, the only important thing is to maintain the process of adapting to a stochastic and changing world. Such an approach would imply very different conservation strategies from what is the dominant approach today. On the other hand, views on conservation have changed a lot in the past [Haila 2012]. It seems to me that orienting somewhere along the middle between these two perspectives may be an appropriate strategy." (Klaus)

This consideration points toward another, dynamic source of uncertainty in conservation: we are facing a big question mark on how to improve the correspondence between human-induced changes in the environment with the dynamics of crucial habitat features critical to particular groups of organisms – across a range of temporal scales (Haila 2007).

3.5 What about ecosystem services?

Ecosystem services are relative newcomers in the conceptual repertoire of conservation biology. It is not self-evident that the goal to safeguard ecosystem services is congruent with the goal of biodiversity protection (see Harrington et al. 2010 for an overview). Some people fear that an emphasis on ecosystem services will result in a loss of biodiversity from sight (Skroch and López-Hoffman 2009; Henle et al. 2012). If we primarily want to extract something out of nature, we do not necessarily need biodiversity. The concept of ecosystem services is essentially based on human valuation systems, which are often equated quite narrowly with changing consumer preferences, willingness to pay, and technological advances (Vira and Adams 2009). If such a utilitarian view dominates and biodiversity is ignored unless it provides us with services, then one can reasonably say: get rid of most of it. This is likely to happen, at least at some scales.

Also, ecosystem services can be specified using several criteria that may be connected with biodiversity in different ways. Biodiversity and ecosystem services are often clearly coupled, but problems arise when measures to protect ecosystem services have contradictory effects on biodiversity (Cardinale et al. 2012). This brings uncertainties in the form of trade-offs into practical management decisions: an operation aiming to achieve a particular benefit may be harmful to other benefits.

"Biodiversity and ecosystem services are very different; the Intergovernmental Platform for Biodiversity and Ecosystem Services (IPBES), for instance, considers them as two separate issues, exactly so they don't compete with each other. What I like about both terms is that at least as ideas, they are both scale-independent. But questions arise when you try to measure either of them. The measures have to be scale-dependent. You cannot measure biodiversity on the global scale in the same way you would monitor changes on local scales. Neither can you consider the same set of ecosystem services, and their fluxes, at the local or global scales. --- So, if we can, at least, agree that the concepts of biodiversity and ecosystem services are both important at a given scale, then we can reduce some of the uncertainty that could come up if we try to always link the two concepts as if they were equal." (Guy)

4. Social and political reception

4.1 Institutions and governance

The adoption of formal institutional devices, such as laws and policy documents, create uncertainties as well. Unclear goals, or goals imposed from above, can create significant conflicts and legitimacy problems (Keulartz and Leistra 2008). Also, there is considerable uncertainty in policy processes and their outcomes. Command and control regulation may backfire (Holling and Meffe 1996). The problems may also induce decision-making frames with a significant degree of discretion for those implementing laws. Informal institutions, such as habits, contact networks, and working traditions, produce further sources of uncertainty in the shape of conflicts or trade-offs between policy, law, and implementation. As Brian Wynne (1992) in particular has convincingly argued, the trustworthiness of public institutions is an essential factor influencing public perception of risks.

"But on the other hand, talking about the uncertainty of institutions gets often far too general. Institutions were actually created to reduce uncertainty in social life. But failure is always possible; analogously, we have market failures, we have state failures, and so on. I think this brings forth one dimension of uncertainty in social life. Furthermore, you may have a rule in social life but you cannot really predict whether people follow this rule. Perhaps it is followed as a statistical pattern, but you can never predict whether specific persons behave in a specific way." (Christoph Görg)

Conditions of stability and predictability of social institutions raise general questions concerning good governance. It is not obvious what the ideal relation between good governance and uncertainty should be. Uncertainty is a pervasive phenomenon in social life in any case, so the question of whether to reduce uncertainty or cope with uncertainty becomes particularly acute in this context.

"We can say that we have a good governance process when the process itself is good, when its output is good, and/or when the outcome, i.e., the consequences of this process are good [Rauschmayer et al. 2009]. Different criteria are used as to what we mean by good. For example, we can say that a process is fair when everybody has a chance to raise voice, which in an extreme case would agree with the Habermasian ideal of discourse ethics, free of domination. --- We could also say a process is good if it leads to a good output such as a binding agreement. But one could also claim that what is really relevant are the consequences that process and output have on the ground." (Felix)

The scale of the political governance system and the size of administrative units it covers matters as well (Haila 2002, Meadowcroft 2002). There are inherent uncertainties in management; what is to be managed is not only the system, but also the reaction caused by the governance process itself. This situation calls for learning and adaptive management (see, e.g., Holling et al. 2002). Adaptive management requires flexibility and reflexivity, i.e. the capacity to make new kinds of decisions when new information emerges or conditions change. However, regulatory decisions should be predictable and the rights and duties clearly defined (Craig 2010, Ruhl 2011). Normative elements are at the background of actual policy measures and the legal rules they build upon.

"Every policy strategy, every law is always a compromise, built upon different interests and power relations related to such interest. A law or governance measure in itself is not good governance, but it is real governance. It includes some interests and power relations and so on, but we have to reflect in a normative way on how to improve this." (Christoph)

4.2 Assessing governance success

A difficulty with assessing consequences of particular governance measures, such as the process of designing the Natura 2000 network or reforming the Common Agricultural Policy in Europe, is that the effects of specific conservation measures get diluted over time into changes in the society due to other kinds of processes. The temporal scale is important in this context. Big changes do not take place overnight. In fact, 20 or 30 years may be a very short time for essential change to take place. We ought to think more in terms of social and political dynamics, their temporal matching and mismatching, and their mismatching with ecological processes (Cumming et al. 2006, Henle et al. 2010).

"I very much like the idea of starting with accepting knowledge gaps and, despite this, realising that we have to do something. It is more motivating to look at processes instead of necessarily looking at the final outcomes. We have the same problem in ecology where sometimes we simply need to find some rules that govern the system, because such rules are more robust to uncertainty. --- We also need to consider trade-offs, for instance in the case of inefficient funding: we may put a lot of efforts into conservation and restoration but they fail because of a parallel process which may be more effective, and completely contradicting the first one. I think that agri-environmental schemes are an excellent example [Henle et al. 2008]. Governments put a lot of money into agri-environmental schemes, but in parallel put about ten times more money into intensive agriculture, which wipes off possible positive effects [Pe'er et al. 2014a]. This definitely increases uncertainty in the realm of governance." (Guy)

A possible approach to assess the uncertainty, which is inherent to policy instruments, is to take the aims at face value (for literature on environmental-policy evaluation, see e.g. Birnbaum and Mickwitz 2009). If the objective of a particular instrument is straightforward, we might check afterwards whether the outcome was as it was meant to be. This possibility would be one characteristic of a successful policy closure [Sect. 5.1].

However, policies can change so quickly that indicators on what follows on the ground are lagging behind. The time-lag in feedback from policy to on-the-ground actions not to speak of time-lag in ecosystem processes is a critical aspect of uncertainty when it comes to informing politicians about what is effective and what is not. People who live close to nature often know very well the systems their sustenance depends on, and should be heard. They also often have good intuition on how different policies influence their livelihood.

Also, objectives of various policies may be diffuse to start with, and they may have been designed specifically to be diffuse to decrease tensions between different sectors of administration. Or there may be sheer lack of coordination between the sectors. For example, many agricultural and other subsidies are contradictory to biodiversity policies (Henle et al. 2008).

"For me the question is: How can we provide guidance to improve the governance of biodiversity, not governance in general? Are we far enough that we can say something specific, or can we merely offer a list of potentially important things without giving specific advice? --- Probably there is no single rule how to assess the governance process for improving chances of success. And also, probably we need different tools depending on the main goal, so perhaps clear diversification of goals and assessment of their synergies and incompatibilities is a good idea." (Klaus)

4.3 Economic instruments

The protection of biodiversity touches on economics in several ways. First of all, effectiveness and efficiency of policy instruments as well as their distributional effects need to be considered. Management measures produce costs through effects on accustomed sustenance that may be hard to evaluate in advance and, with an even higher degree of uncertainty, the measures might also produce benefits. Whereas costs of biodiversity conservation, in the form of opportunity costs associated with land-use restrictions or of direct management costs, mostly accrue to local actors, conservation benefits often reach far beyond local and regional boundaries (Perrings and Gadgil 2003, Ring 2008). Furthermore, the costs and benefits are not distributed evenly among stakeholders, e.g., public versus private, or rich versus poor.

As a consequence, various types of regulatory and economic instruments must be included in the toolbox of biodiversity management (Ring and Schröter-Schlaack 2011). Market-based instruments are often specific enough to be amenable to empirical follow-up. In settings with good closure, cost-benefit-type calculations can certainly be valuable, albeit with reservations because the temporal horizon is restricted. Ecological economists have argued that current market prices give a notoriously unreliable standard for calculations covering any length of time into the future. Therefore, apparent precision of monetary estimates is deceptive (Spangenberg and Settele 2010).

The strict requirement of cost-benefit optimality can be relaxed, but indicators and qualitative measures are necessary, and applying an evolutionary perspective to policy-making rather than a static-equilibrium-oriented perspective helps in this context (Ring 1997; van den Bergh and Gowdy 2000).

"We don't know the optimal solution at a certain point in time. It is more important to try as far as possible to move into the right direction, if you can say what the right direction is. This is relevant for the precautionary principle: it is easier to find the right direction than try always to do the optimal thing. Adaptive management builds upon a similar idea: if you are able to at least measure some properties related to sustainability, we should be able to see whether a course of action will lead in that direction, more or less." (Irene Ring)

Another major issue is that all goals cannot be reached everywhere at the same time: priorities have to be defined, and choices have to be made, at least in part by weighing costs and benefits. This creates uncertainty: Are the weights appropriate? In this context, Maclaurin and Sterelny (2008) make a good case in favour of using *option value* as a framework, i.e., assessing potential benefits of preservation on a long temporal horizon, uncoupled from immediate market valuation. Estimating option value brings uncertainty about the future explicitly into the assessment. Maclaurin and Sterelny (2008) showed by examples that specification of the options created by biodiversity, leaning on empirical knowledge to the extent possible, helps to reach a decision despite uncertainty. Through this effect, as they note, " (t)he crucial point about option value is that it makes diversity valuable." (p. 154).

The use of option value as a framework is a close kin to another decision rule recommended by economists in a situation of uncertainty: the strategy of the second best, i.e., setting goals that are more robust than the calculated optimum, which may be unattainable anyway (Lipsey and Lancaster 1956-1957, Majone 1989).

4.4 Precaution

The precautionary principle originated in the context of environmental policy and the volume of the literature on the topic is huge (as an introduction, see Harremoës et al. 2001, EEA 2013). Biodiversity loss has received its share (e.g., Cooney and Dickson 2005), but the relevance of the precautionary principle clearly varies across policy fields. It is central in the case of health and hazardous chemicals (e.g., Kriebel et al. 2001), but its applicability in biodiversity is more ambiguous.

"The precautionary principle is tricky and allows different interpretations. There was a huge contestation between the United States and Europe on what the precautionary principle exactly means in the biodiversity convention and the Cartagena protocol. It is not only about uncertainty, it is more about the possible impact of something that we perhaps do not really understand." (Christoph)

The demand for precaution is the more convincing the better we can delineate alternative options and their concomitant uncertainties, but it is relevant also under less stringent conditions (EEA 2013). The complexity of biodiversity issues means that we can only give relatively general rules on what is relevant and what is not. Above all, it is imperative to increase understanding of what different instruments mean for the real world if they are enforced.

"I think that the protection of biodiversity and maintenance of ecosystem services can potentially go in opposite directions as regards the precautionary principle. Conservation of biodiversity is based on the assumption that we should protect biodiversity for its own sake, in accordance with the precautionary principle. We assume that it is beneficial also for humans, but it is valued for its own sake. However, in the context of ecosystem services attention to biodiversity is conditional upon its effect on specific ecosystem functions." (Jukka Similä)

In other words, in the latter case uncertainty is more troublesome: we want to know what the service in question is and reduce uncertainty as to what actually follows when we protect a certain asset. Notwithstanding, as regards systems poorly known, precaution will remain a very important principle.

4.5 The concept of biodiversity and its surrogates

Ultimately, the aim to protect biodiversity has to make sense to a broad public that forms an *active public*; an idea building on the classic formulation of the dynamics of publicity by John Dewey (Dewey 1927; see Hajer and Wagenaar 2003). Assessing the conceptual basis of the biodiversity concern can give rise to different opinions

(Maclaurin and Sterelny 2008). Conceptual confusion may contribute to general uncertainty about the relevance of the issue.

“What is biodiversity? There is some conceptual ambiguity. First of all there is often uncertainty about proper objects of research and management. Is it species numbers, is it genetic variability, or is it life on Earth? This gets down to the question: What are the goals of conservation efforts? A specific question in this respect is how to deal with exotic species [Davis et al. 2011, Simberloff 2011]. --- This ambiguity has been enhanced and made even more difficult on the normative side by the connection between biodiversity and other equally ambiguous terms like ecosystem functioning or ecosystem services. So the relation between biodiversity and ecosystem functioning has increasingly come into the discourse about biodiversity. We’re threatened by a vicious circle: protect biodiversity to maintain ecosystems, and protect ecosystems to maintain biodiversity.” (Kurt Jax)

One way to clarify the confusion is to draw a distinction between the brief characterisation of biodiversity in the Convention on Biological Diversity versus problems that arise when it is applied to policy or management. On general terms, the brief definition provided by the convention can be considered clear and quite satisfactory, but it does not easily transform into guidelines.

“We need to decide which components of biodiversity we want to focus on. A number of policy documents are not clear about this. For instance the goal of higher biodiversity to me is meaningless.” (Erik Framstad)

This source of uncertainty demands that one should clearly recognise the context in which the term biodiversity is used as an argument. The term may give rise to problems as biodiversity can be operationalised in alternative ways (e.g., Sarkar and Margules 2002). There is no simple way to conclude which one is most productive. Perhaps there is also linguistic vagueness because the way we use terms varies a lot. Linguistic and terminological variation thus brings another element of uncertainty into the game.

“Another issue is how much power and weight different parties have in the discussion [Latour 1987]. There are so many different ways of aggregating multi-criteria matrices to forge indicators of biodiversity that very often people lose any idea of what the weights mean. A really important aspect is that there is no objective way of deciding which indices should be used. --- I think some of these discussions come up in monitoring in an analogous fashion. The problem always comes up: What should we monitor? We want to monitor biodiversity. And then somebody is monitoring some components of it, and somebody else says that you are not monitoring biodiversity. Often, both are right.” (Klaus)

Seemingly, uncertainty about what biodiversity is may create serious confusion with respect to what to monitor, where and how (Henle et al. 2013). In this context, reducing uncertainty would be highly welcome.

5. Communication and societal relevance

To succeed in the aim of protecting biodiversity, conservation biologists need to learn to get their message through. When exploring the concept of causality, Herbert Simon (1977, p. 52) noticed that in a social context causality is analogous to what physicists have called "action at a distance", i.e. material interference without an immediate physical contact. He continued the line of thought with an aphoristic remark: "no influence without communication".

This idea is worth taking seriously. However, it is self-evident that communicating the need to protect biodiversity to the society at large is much more demanding than merely spreading a message. To become influential, the communication has to strike a cognitive chord.

5.1 Aiming at closures, albeit temporarily

A specific message needs a specified context. This principle corresponds to the demand that satisfactory closure conditions are necessary for a satisfactory scientific explanation (Dyke 1988). Similarly, closure conditions are important in formulating policy guidelines that can be implemented (Hajer 1995), especially in the short term when concrete decisions have to be made.

To further specify this demand, we can use Herbert Simon's (1981, p. 190) characterisation of the idea of "bounded rationality" as " (t)he meaning of rationality in situations where the complexity of the environment is immensely greater than the computational powers of the adaptive system." This description certainly fits situations in which choices have to be made between alternative ways of protecting biodiversity: Draw together all relevant knowledge you have, and do the best you can. On a longer temporal horizon, it is important to value chances for flexibility, potential for making new choices in new situations.

A too hastily formed closure is, however, vulnerable to type III error: answering the wrong question (Dunn 2001, Kriebel et al. 2001, see Haila and Henle 2014). Or, in other words, the answer may connect to an unproductive contrast space (Garfinkel 1981, Sect. 2.1 above, Haila and Henle 2014).

Depending on the nature of the closure, the concomitant uncertainty is bounded as well. The better the understanding of the structure of a system under research, the more uncertainty is bounded (Smith 2007). That is true also of the ontological dimension of uncertainty. When modelling the variability of a particular ecological system, one cannot expect a huge change in the values of relevant variables in a very short time. Furthermore, we know well enough basic population dynamics of different kinds of organisms to formulate realistic expectations, for instance, in a comparison between the population growth rates of lemmings versus polar bears.

"Differentiation between goals might help and trigger fruitful discussions. There are certainly policy goals, which have obtained so good a closure that it does not matter what the values of the people are. For instance, speed limits on motorways. Just make a speed limit and it does not matter what people think. After a new rule is enacted, people change their ways and values when they learn to follow the rules. Norbert Elias called this the technisation of society [Elias 1995]. But one could draw distinctions between different kinds of governance processes, depending on the clarity of the closure [Haila 2008]. Actually, closure is a pretty good notion for analysing such situations." (Yrjö Haila)

However, closure is always temporal and contextual. Any proposed closure can be challenged, and established closures can be opened up to further consideration. Speed limits may be lowered in residential areas, in the vicinity of primary schools or fire stations, and so on. A historical demonstration of changes both in closure and norms is offered by regulation of hunting and species protection (Pohja-Mykrä et al. 2005, Haila 2012, Klenke et al. 2013).

5.2 Enhancing public discussion

Uncertainty can serve as an entry point to discussions, even concerning quite complicated issues, such as the relationship between ecosystem services and biodiversity. Uncertainty may play an important role. It is a question of communication, how we can use uncertainty instead of blowing it up all the time to levels where we just do not communicate at all (see Pe'er et al. 2014b).

We also need to take into account the potential that uncertainty offers for opponents of environmental concerns, as the example of climate sceptics shows (UCS 2004, Pielke 2005). Another aspect to take into account is emphasized by ecologists communicating with conservation NGOs about potentially misguided actions that may turn counterproductive. Improved understanding of the sources of uncertainty might show ways toward reconciliation of opposing opinions (Chris Margules, personal communication].

"For raising awareness about specific problems, uncertainty may create difficulties, but it may stimulate public discussion. But if you want to define policy strategies you have to look for costs and benefits, you have to look for side effects, and therefore you need some knowledge. --- It is much better to communicate uncertainty than to speak with a strong conviction: this is the result, this is the truth, the scientific truth." (Christoph)

It is well known that conflicts can also provide entry points to fruitful discussions. This, however, depends on the nature of the conflict. For instance, the establishment of the Natura 2000 network in the EU has given rise to local conflicts in several countries. If such conflicts lock in as contests of prestige between authorities and local inhabitants, the consequences may be mainly detrimental, and this is what largely happened in Finland (Hiedanpää 2002, Björkell 2008). A similar case was reported from Poland:

"Then the main approach of regional administration was to engage local politicians and authorities into consultation programs to try to talk to them and perhaps manage the conflict a little bit. A source of uncertainty at this stage was the relevance of social conflicts. Then there was new recognition of importance of local communities, especially landowners and people in charge of community-owned land at the municipal level. We as a research team tried to provide the authorities a diagnosis of the local conflicts of opinion, or at the very least insight into the consultation process and the role of stakeholders, but the policy priorities were different. If the focus on managing conflicts and landowners and local communities had been present from the beginning, the process might have looked quite different." (Joanna Cent)

Given a communicative start, however, conflicts could become occasions of mutual learning. Local conflicts have the potential of bringing specific questions into focus, such as how to combine biodiversity preservation and local livelihoods.

"A potential conflict might bring different opinions into the open; for instance if nobody knows in advance what different stakeholders think about, say, the Natura 2000 process and what the consequences are for them. A research project functions almost like an intervention. --- And so such a situation is a fantastically interesting case of the potential of using uncertainty to enhance fruitful discussions. In fact, the process in Poland took quite a long time, something like five years. There would have been enough time for fruitful communication." (Yrjö)

5.3 Deliberation and social learning

According to the view of political scientist Maarten Hajer (2009), deliberation is primarily about defining the meaning of different policy alternatives. Scientists can support such a process by being aware of the possibility to adopt alternative roles in public discussions.

"Negotiations are possible, based on the common ground, eventually. The first step, the first stage in order to find common ground and negotiate is to understand different logics, different knowledges, and that basically we scientists are one specialist party, and there are many other people with completely different opinions." (Joseph)

The development of the Nature Index for Norway is an interesting example in that it has a very ambitious aim: to have an instrument to provide an overall assessment of how well Norway maintains nature and avoids loss of biodiversity [Sect. 3.3 above]. With the various statistical and more fundamental uncertainties inevitably associated with the NNI, one may question whether such an objective will ever be obtained. The experts involved in the process expressed concern, but they still considered the resulting index values to be reasonable for their respective ecosystems (Figari 2012). Also, the NNI may have another important role to play as a basis for discussion with various stakeholders about the meaning of biodiversity and our custodianship of nature. By discussing the basic concepts of the NNI, as well as the range of decisions made during the process, stakeholders of various sectors may conduct an increasingly informed debate about nature and biodiversity.

"I've been in this sort of game for 30 odd years, communicating with policy makers and lay people. I'm not sure if I have really taken on the role as an advocate as such, to any great extent. But of course we communicate with different people, within different contexts. If I am talking to journalists or others who need to have a fairly simplified message to their readers, I probably do not spend a lot of time making any complex statement with a lot of uncertainties about this and that. Also, when communicating with bureaucrats who are there to execute policy, we often get criticised for not being clear enough; they dislike that. --- But in the context of the Norwegian Nature Index, we also had a lot of debate with a broader audience beyond natural scientists, particularly on forests, that was really the one nature type where everybody had opinions. We've been going around to local municipalities, talking to the forest managers, the officials at the municipality level, plus representative forest owners. And it's surprising how benign and accommodating they are – it is a process that seems to be leading to greater consensus about the aim of the project, and how it can be useful." (Erik)

Another interesting dimension of public deliberation has been raised by the potential tension between general goals and specific applications. It is generally assumed that specific topics offer grounds for fruitful discussion, but this is not always the case.

"Under which conditions does collaborative learning work, so that people merge towards a common understanding despite differing goals, and when it doesn't work? What does this difference mean for our approach in the management? An example I can give is a study in the context of a conflict on the establishment of a nature reserve in which the utilisation of different spatial representations were compared. When they used virtual spatial experimentation that was not representing the real case study, it worked. But when they used the real map this was not helpful. People were too concerned to secure their own claims and not open to look for solution where all would be better off. [Barnaud et al. 2013]" (Birgit)

6. Conclusions: collective effort with a division of labour

Biodiversity praxis draws upon a diverse combination of specialised skills that range from field work and data analysis to formulating management targets or policy goals and lobbying for implementation. As Pielke (2007) points out, scientists can adopt different roles when interacting with society at large. Our aim in the Leipzig workshop reached further, however. In addition to discussing what kinds of different identities scientists can adopt, it is crucial to establish fruitful interactions among scientists who have adopted different roles. The notion of semantic space helps in this regard. Scientists, managers and policy-makers specializing in different aspects of biodiversity praxis could address together such aspects of uncertainty that are closest to their respective expertise. In particular, identifying dimensions of the semantic space of uncertainty in biodiversity praxis may facilitate collective learning (Haila and Henle 2014).

The semantic space is multidimensional. Haila and Henle (2014) presented a preliminary scheme with five dimensions: [i] data; [ii] proxy; [iii] concepts; [iv] targets, policy and management; [v] normative goals. In this scheme, however, societal aspects are collapsed together. One could easily add several more dimensions – until the whole structure becomes intractable. Uncertainty is a cluster concept, all types of uncertainty cannot be addressed simultaneously. A more fruitful possibility to make the idea of semantic space usable in practice is to reduce the dimensionality "step-by-step" by specifying what kind of interactions can be distinguished among a specified set of dimensions.

Managing Natura 2000 sites offers an example. On the one hand, there are field surveys, and reports offering conclusions on the conservation values of any particular site. On the other hand, there are needs and wishes of local people and visitors. The problem is to fit these two sets of factors together.

"Of course, if it is an absolutely unique site, then there is no way to undermine the idea that this is a valuable site that has to be preserved. But if it's not, as Natura areas usually aren't, then there are potentially other things to consider, also compensatory procedures. So it's not only that the conservation goals should be watered down, it's also that conservation goals can be enriched by some kind of societal considerations." (Yrjö)

The accustomed methodology of scientific research includes elements that point toward cooperation that promotes learning. Our task is to grab the opportunity.

"What we are mostly discussing is basically a scientific cycle within science. But then we also have the societal cycle, which is as large if not much larger – society with its own processes, or if you want, socio-economics. --- The stronger the links are, the more adaptive, for instance, management can be. So the idea of participatory modelling, for instance, is that the process itself is more compact. That's the process also of developing good monitoring, or a good index: to put more and more people together, and then perhaps we can pack the societal and scientific processes, to get more adaptive and quicker, and better respon to uncertainty." (Guy)

Also, work on the local level offers other kinds of potential openings for fruitful learning processes. There is a discrepancy that stems from the generality of global recommendations and the specificity needed in local contexts.

"The problem of scales becomes acute when you think the (local) system you are working with is closed, but it's not, and that means that what you are doing is not achieving what you believe it will achieve. So the question for me here is not how you can make sure that the information from the outside gets into the local scale. Rather, the question is, how can you provide those who work on the local scale good enough guidance on when they have to go outside of the local scale, and when they can work on the local scale. --- Even if it's not essential for the particular case they should at least be aware that a larger scale exists." (Klaus)

Finally, the normative background of the concern over biodiversity requires attention because it gets mingled with all other dimensions of biodiversity praxis. Biodiversity preservation is basically a normative principle. It has a very strong material basis in the human biospheric dependence, but the normativity breaks through because there are always several ways to reach particular goals, the more so the more general the goals (Haila 2004, Maclaurin and Sterelny 2008). In other words, biodiversity protection is ethically driven, throughout. This challenge has a pragmatic side, too: the value of ecosystem processes and biodiversity has to be integrated into our perception of economic and social development.

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Uncertainty and the design of in-situ biodiversity-monitoring programs

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Abstract

There are many techniques to deal with uncertainty when modeling data. However, there are many forms of uncertainty that cannot be dealt with mathematically that have to be taken into account when designing a biodiversity monitoring system. Some of these can be minimized by careful planning and quality control, but others have to be investigated during monitoring, and the scale and methods adjusted when necessary to meet objectives. Sources of uncertainty include uncertainty about stakeholders, who will monitor, what to sample, where to sample, causal relationships, species identifications, detectability, distributions, relationships with remote sensing, biotic concordance, complementarity, validity of stratification, and data quality and management. Failure to take into account any of these sources of uncertainty about how the data will be used can make monitoring nothing more than monitoring for the sake of monitoring, and I make recommendations as to how to reduce uncertainties. Some form of standardization is necessary, despite the multiple sources of uncertainty, and experience from RAPELD and other monitoring schemes indicates that spatial standardization is viable and helps reduce many sources of uncertainty.

Keywords

Biodiversity, stakeholder, sampling, identification, detectability, distribution, remote sensing, concordance, complementarity, stratification, data quality

Introduction

There are many sources of uncertainty in scientific research, some of which can be modeled mathematically, but some sources of uncertainty are considered non-probabilistic, and the best way to deal with these is controversial (e.g. Sniedovich 2014). Some uncertainties can be reduced by careful quality control during data collection, but most researchers attempt to reduce uncertainty by statistical analysis, usually through model-based inferences (Gitzen et al. 2012, Thornton et al. 2014). There is an enormous literature on model-based inference (e.g. Anderson 2008), but even the most complex of these models, with many alternative hypothesis, relate to only very simple systems with limited inputs and outputs. They are good for evaluating sources of uncertainty that can be modeled by probability distributions, and in essence are usually just attempts to parameterize a given generic model. For example, Anderson (2008) used Caley's and Hone's (2002) study of tuberculosis transmission in ferrets as an example of a multi-hypothesis study. However, all of the hypotheses presented related to ways that ferrets could contract bovine tuberculosis. These are very interesting questions, but a biologist interested in biodiversity questions might have to deal with uncertainty as to whether bovine tuberculosis is better avoided or treated, whether management costs outweigh the costs of no action, whether other species are more important than ferrets in transmission, whether control measures might be considered inhumane, whether climate change or changes in markets might make the question irrelevant, and many other sources of uncertainty that are difficult to put into a probabilistic framework. While it is reasonable to ignore such concerns in a short-term study designed to find a solution to an immediate pressing problem, researchers interested in conserving biodiversity over the next century do not have the luxury of being able to use such a focused and short-term approach (Haila et al. 2014).

Ecologists are generally most worried about uncertainty in relation to their field of research. Taxonomists worry about the correctness of identifications, modelers worry about the accuracy of parameter estimates in their models, sociologists are concerned with uncertainties about the contributions of different stakeholders, geneticists try to reduce uncertainty about gene flow, etc. However, biodiversity managers have to deal with all sources of uncertainty simultaneously, and the importance of different forms of uncertainty will vary depending on the objectives of management. I have therefore adopted a very broad concept of uncertainty, and make recommendations as to how they can be reduced or quantified by planning during implementation of field infrastructure and quality control during data collection.

Here we will describe some of the sorts of uncertainty that we had to take into account when developing the RAPELD system of biodiversity monitoring (Magnusson et al. 2005). We will use that system to illustrate the issues, but the same considerations are applicable to any *in-situ* biodiversity monitoring system. The RAPELD system is a standardized monitoring scheme developed to allow integrated analyses of biodiversity data collected in rapid assessments (RAP) and long-term (LTER [PELD in Portuguese]) studies (Costa and Magnusson 2010; Magnusson et al. 2013). Sampling in the RAPELD system is based on spatially standardized transects and plots, reducing uncertainty about spatial interpolations and extrapolations. The system can be adapted to different sized areas of interest, but, because it is modular, statistically valid comparisons can be made between studies that originally used different combinations of spatial modules.

The basic sampling unit in the RAPELD system is a 1 km transect combined with one or more permanent plots that are usually 250 m long in the largest dimension. That is, the system was designed for the relatively large landscapes managed by most municipal, state and federal governments, and is often not appropriate for the small-scale landscapes studied by many academic biologists. Uncertainty about the scale at which users would apply the results was the prime reason for designing a modular system.

Although there is large variation in the sizes of RAPELD modules, most users use a standard 25 km^2 grid with 30 uniformly distributed plots for intensive studies in long-term ecological research sites located near major research institutions, and standard 5 km^2 (5 km × 1 km) modules with 10 uniformly distributed plots for RAP studies or long-term studies distributed over large areas (http://ppbio.inpa.gov.br/inventarios/modular). Uniformly distributed plots are 250 m long and the center line follows the altitudinal contours (http://ppbio.inpa.gov.br/instalacao/parcelas), a design that generally allows greater precision of models that relate biodiversity parameters to environmental variables. Plots for special strata, such as streams and riparian zones, are distributed in proportion to their occurrence in the landscape.

Most biologists specialize in a limited range of taxa (e.g. vascular plants) or processes (e.g. pollination), but decision makers have to take into account the needs of many different stakeholders, who may be interested in subjects as varied as the effect of large carnivores on domestic animals, bacterial metagenomics, ecosystem carbon storage and traditional uses of biodiversity. Reduction of these varied interests to a production-line mathematical model with limited inputs and outputs is usually not feasible, especially when a major uncertainty is whether we are addressing the right question (Haila et al. 2014). Therefore, investing monitoring in a limited number of questions, however important they may be at the moment, is not an efficient strategy.

A major difficulty, perhaps the major difficulty, with the interpretation of data collected in monitoring exercises is that the biologists have focused on their favorite group and not collected the data in such a way that it can be integrated with information generated on other biological groups and presumed environmental drivers. Different taxa provide different information about the distribution of biodiversity, and there is often heated discussion about the appropriate group to study (Magurran and McGill 2011). However, the sad reality is that we generally just base our decisions on convenience. There are few groups that have been surveyed over wide areas for which we are reasonably confident that most individuals have been correctly identified. These are usually only birds and vascular plants, though some groups of butterflies and mammals are reasonably well known in some areas. There is strong evidence that they are not sufficient to represent all biodiversity (Caro

2010), but they will continue to do so until we move out of our comfort zones within the internet cloud.

When we started our studies, discussing possible sampling designs only resulted in endless discussions as to which design optimized for a particular question was the “right” design. We found that the only way to obtain integrated data collection was to provide standardized infrastructure that could be used by most researchers to answer a wide variety of questions. Henle et al. (2006) present a European example of this approach, and Olsen et al. (2012) give several examples from the USA. Most researchers had not adequately budgeted for field infrastructure and were happy to use what was available. As this infrastructure had been designed to allow integration, data collection resulted in integrated studies almost as a side effect (Costa and Magnusson 2010, Magnusson et al. 2013).

There is a great difference between planning for an individual study of a limited range of organisms and planning a monitoring system for a wide range of taxa over very large areas. We did not appreciate this at the beginning, and it only became obvious to us as we saw what worked for a wide range of researchers over large areas, and what was mainly useful for specific studies. This dichotomy has been recognized by many researchers responsible for nationwide monitoring of biodiversity (e.g. Johnson 2012, Olsen et al. 2012), but has only recently been included in reviews of best monitoring practice from a statistical perspective (e.g. Buckland et al. 2011, Connolly and Dornelas 2011, Reynolds 2012), most of which had previously concentrated on idiosyncratic planning of projects with a common source of funding (e.g. Likens and Lindenmayer 2011). Below I will provide a short overview of key sources of uncertainty and how standardized field infrastructure can be used to help avoid or quantify uncertainty during the establishment and running of large-scale monitoring schemes.

Uncertainty about the stakeholders

Individual researchers tend to consider their study site to be primordially of interest in relation to their current research question. However, that piece of land may have a multitude of other values for the local people (Silvius et al. 2004). When planning where to install long-term research sites, we found that many different stakeholders were interested in the same site. Data generated might be used by international organizations, such as the International Long Term Ecological Research program and United Nations agencies, federal agencies, such as ministries of science and environment, regional bodies, such as State Government planning agencies, individuals operating regionally, such as university professors, park administrators and firms specialized in bioprospecting, and those interested in a small patch within a site, such as students, community groups and volunteers. In general they follow a political hierarchy (e.g. Magnusson et al. 2013: 58-59), but the categories do not always have clear boundaries. For example, individual volunteers may contribute to nation-wide projects, such as Christmas bird counts.

Stakeholder roles also depend on their position in the hierarchy. Multinational bodies try to influence decisions by changing national policies. Most funding agencies for long-term monitoring are national, but international organizations may provide short-term funding. Federal and state governmental agencies generally try to manipulate people´s behavior through the legal system. Academics are involved in planning and analysis, and most of the long-term monitoring has to be done by local people or students. All of these categories have fuzzy boundaries, and the relative interest of these groups is likely to change depending on unpredictable factors, such as employment opportunities, market demand and global climate change. Nevertheless, a monitoring scheme has to take into account the different roles of stakeholders. Probably the most difficult aspect of developing the RAPELD system was ensuring that different actors in different levels of the political system would be satisfied with their role, and the roles of other actors (Magnusson et al. 2013).

Biological relationships with distance are not linear (Landeiro and Magnusson 2011, Magurran 2011, Rosenzweig et al. 2011). It is possible to scale up from local data to larger areas, but only if data are collected in spatially standardized arrays, and this may create conflicts with organizations and volunteers who collect the data (Turnhout and Boonman-Berson 2011). Relationships depend heavily on the sampling scale (Baccaro et al. 2012, Rosenzweig et al. 2011, Chisholm et al 2013). Evaluations of the effects of scale of sampling are generally difficult with idiosyncratic sampling, but can be achieved with a few sites with standardized infrastructure. Where coverage is inadequate, geostatistical techniques may help to define priorities for locations of new sampling sites (Lin et al. 2008). Modular designs allow flexibility in answering local questions, while permitting different stakeholders to adjust the system to their questions (Magnusson et al. 2013). Some RAPELD sites, such as that in the Virua National Park, have been used both for local studies of interest to park managers (e.g. Pontes et al. 2012) and included in cross-site comparisons for academic studies (e.g. Souza et al. 2012).

Uncertainty about who will monitor

Different stakeholders have different human and financial resources, but very few have the capacity to undertake detailed studies over large areas. Therefore, we needed a system that would allow integration of a large number of stakeholders with different technological tools at their disposal. Our infrastructure is suitable for use by local people with no formal education, and their participation is often vital because much biodiversity is hidden from the eyes of casual visitors (Magnusson et al. 2013).

Students are the main researchers in most RAPELD sites, but many of the surveys carried out in the modules around the Santo Antônio hydro-electric dam were undertaken by parataxonomists who had been trained in another state. We found that there was a trade-off in sources of uncertainty. Monitoring by students and volunteers increases uncertainty as to the frequency and quality of monitoring. Relying on surveyors specifically contracted for the task, as was the case in Santo Antônio, increases uncertainty as to whether funding will be sufficiently reliable to meet labor-law requirements. By concentrating on field infrastructure, we were able to take advantage of different forms of financing for monitoring in different places and time periods.

Costs of monitoring could not be too great if different stakeholders with limited economic resources were to be involved, but the system had to house high-technology systems, such as eddy-flux towers, when available. While it is not possible to foresee all stakeholders, it is possible to provide field infrastructure that most will need, such as access trails and permanent plots.

Uncertainty about relations with remote sensing

Because of its complexity, all aspects of biodiversity cannot be measured directly and decisions are made based on surrogates, which are usually maps derived from remote-sensing data, but may be simply the representation of one biological group by another. For instance, vascular plants are often used to identify "habitats", "ecoregions" or "ecosystems" that purportedly represent boundaries to the distribution of other organisms, such as insects, mammals or fish (e.g. Olson et al. 2001, Higgins et al. 2005). The technology is continually advancing, and it is not possible to predict what remote-sensing products will be available in the future, but the greatest sources of uncertainty at the moment relate to the relationships between surrogates and the target organisms in which we are interested (Magnusson 2004, Franklin 2009, Caro 2010).

Biologists generally stratify and collect only where they "know" that certain types of organisms occur (Henle et al. 2006). When they are forced to sample regularly or randomly because that is where the infrastructure is, they almost always discover that their preconceived ideas were wrong (Oliveira et al. 2008), including ideas about the relationships between species distributions and remote-sensing surrogates. Other researchers involved in country-wide programs have found a priori stratification to be problematical (e.g. Johnson 2012, McDonald 2012). Infrastructure that is not dedicated to particular groups reduces the risk that spatial sampling will be dedicated to a particular taxon. Standardized infrastructure in RAPELD plots has allowed validation of surrogates for which geographic information system (GIS) layers were available (e.g. Schietti et al. 2013).

We were initially uncertain about both the questions that stakeholders would want to answer and the remote-sensing technology that would become available. However, most political decisions are made on scales of tens to hundreds of linear kilometers, and few researchers have the resources to use remote-sensing tools with pixel sizes of a few meters. Therefore, we designed a system with relatively large sampling units (250 m long plots and 5 km long transects) that would allow the use of a wide variety of remote-sensing products available today, and will allow the use of even more in the future as products with smaller pixel sizes come on line.

Uncertainty about what to sample

Many monitoring programs have fixed targets, such as the Alberta Biodiversity Monitoring Institute (ABMI – Haughland et al. 2009), the Center for Tropical Forest Science (CTFS – Condit 1988) and Tropical Ecology, Assessment and Monitoring (TEAM – Martins et al. 2007). Standardization of a limited range of targets (e.g. vascular plants in CTFS plots) facilitates standardization, but leaves much biodiversity without coverage. Standardization for many groups (e.g. ABMI and TEAM) greatly increases the costs, and all standardization of targets reduces the range of stakeholders who will participate and the range of questions that can be answered. Therefore, we developed a system that permits essentially all elements of biodiversity to be monitored, but does not require that all targets are monitored in every site.

Integration can be obtained by associating individual sites with larger initiatives for particular targets. For instance, RAPELD plots are included in the RAINFOR (e.g. Emílio et al. 2013), GVID (e.g. Pezzini et al. 2012) and ATDN (Stropp et al. 2009, ter Steege 2013) vegetation networks. The same plots have been surveyed for taxa as diverse as mites (Franklin et al. 2013), ants (Souza et al. 2012), frogs (Menin et al. 2007) and birds (Bueno et al. 2012). There is a logical trade-off. Very strong standardization reduces coverage, but too little standardization makes wide-scale syntheses impossible. Discovering the most appropriate targets for any particular question is an on-going process, so making a design that is only appropriate for one biological group is not an optimal strategy.

Uncertainty about where was sampled

Most biologists now carry GPS devices, and geographic coordinates are the backbone of the Darwin-core system for digitalizing the information in biological collections. However, precise information about collection locations, or a single point representing the headquarters of park personnel in a large reserve are generally not sufficient to evaluate search effort or relate biological data to potential abiotic drivers. When we installed RAPELD modules in areas that had been intensively studied by other monitoring programs, we encountered many difficulties in avoiding disturbance to their plots, because the other programs did not have precise coordinates delimitating their field infrastructure.

RAPELD modules provide researchers with extremely detailed information on the location of trails, plots and large sessile organisms, such as trees. As RAPELD plots are long and thin, it is easy for researchers to locate their organisms quickly using only a compass and a measuring tape. All trails are marked at 50 m intervals (100 m intervals in some older sites), so researchers and local assistants can record relatively precise locations even when they do not have GPS equipment. This has been especially important for the use of RAPELD in environmental-impact studies, because reduction in area occupied is often a more sensitive measure of impact than attempts to estimate absolute numbers of organisms by mark-recapture methods (See “Uncertainty about detection” below).

Uncertainty about relationships

Different aspects of biodiversity and the environment are usually studied by different researchers, and very often it is difficult to see what these researchers have in common. "Integrated" projects usually involve extensive discussion about how the funds will be divided and the general locations of study sites. However, when the time comes for analysis, it is usually impossible to integrate the different studies that were done on different temporal and spatial scales, even though all were contained within the same geographic envelope. Often, researchers from different disciplines have completely different concepts of what represents replication and independence of observations.

By installing a system of transects, and especially plots, that can be used by a wide range of disciplines, we were able to integrate many studies that previously had been considered too disparate for interdisciplinary studies (see also Henle et al. 2006). Almost all studies that have come out of RAPELD systems have integrated data from a variety of disciplines, but have generally focused on a limited range of biological taxa. However, the RAPELD spatial standardization and emphasis on data storage and availability have allowed integrated studies of concordance in the landscape distribution of different taxa (e.g. Landeiro et al. 2012).

Narrow plots that follow altitudinal contours have less internal variability in environmental predictor variables than conventional square plots, or long thin plots that are not oriented along contour lines (Henle et al. 2006, Castilho et al. 2010). This allows much more precise determination of relationships with predictors than possible with standard plots. As important as reducing uncertainty, is that this reduces costs, and allows detection of changes within a shorter period. For instance, Castilho et al. (2010) were able to show significant relationships between biomass accumulation and environmental predictors with 2-yr intervals between tree surveys in a RAPELD grid, at a fraction of the cost of the implementation of a single large plot, even though the differences would have been within the measurement error for a single large plot.

Most studies in RAPELD plots have investigated the relationships between topographic, soil or hydrological variables and organisms (e.g. Menin et al. 2007, Bueno et al. 2012, Baccaro et al. 2013, Emílio et al. 2013, Schietti et al. 2013), but some studies have investigated relationships among different groups of organisms (e.g. Baccaro et al. 2012, Landeiro et al. 2012) and studies are starting to investigate how relationships change over time (e.g. Espírito-Santo et al. 2009, Castilho et al. 2010). However, evaluation of geographic variation in these relationships based on RAPELD spatial designs replicated in different regions has been undertaken for few groups (e.g. Souza et al. 2012, Zuquim et al. 2012).

Uncertainties that can be reduced by quality control

Uncertainty about identifications

Field work is increasingly being considered unfashionable (Magnusson 1994) and many believe that we can resolve all the problems associated with biodiversity by mining digital information on collections. However, the quality of identifications is extremely varied. An internet search for photographs of a given species will often result in photographs of organisms from different genera or even phyla. For bio-diverse groups, such as arthropods, the species may not have been described. Advances in genetic techniques may alleviate these problems for collected specimens in the future, but many surveys, especially of endangered taxa, are based on sightings.

Different observers can result in different diversities, and different levels of biotic complementarity, even for comparisons of the same site. Therefore, we have invested heavily in surveyor mobility, so that different researchers can exchange experiences and compare identifications. Field workshops are much more efficient than learning by reading, and field courses are a large part of our investment <http://ppbio.inpa.gov.br/extensao>. In any case, as many voucher specimens and photographs should be taken as are financially and ethically feasible. Passive sampling by traps may reduce observer biases, and some taxa can only be efficiently sampled with traps. However, passive sampling is often inefficient in comparison to active sampling (e.g. Ellison et al. 2007), and passive sampling usually does not allow precise evaluation of the area sampled by the device, invalidating estimates of the number of species in the area of interest using rarefaction.

Marked plants (live herbariums) may allow re-evaluation of identifications in the future. Production of printed and internet field guides helps maintain stability of identifications across sites, and within the same site through time. For the first RAPELD site, we produced guides to frogs, lizards, the predominant understory angiosperms and ferns (Costa et al. 2008, Lima et al. 2008, Vitt et al. 2008, Zuquim et al. 2008). Guides to snakes, ants and fungal fruiting bodies are in production. Video footage and sonograms help identification of many taxa <http://ppbio.inpa.gov.br/sapoteca/paginainicial>. Where possible, genetic material should be collected and stored, even if resources are not currently available for analyses. The laboratory costs for genetic analyses are dropping precipitately, and exotic and expensive analyses today will be routine in the future. Other techniques, such as near-infrared spectroscopy (NIRS), offer even cheaper solutions (Foley et al. 1998, Durgante et al. 2013). However, if the material is not collected now, we may lose our bench marks.

Uncertainty about detectability

Conservation decisions are made based on the distribution of taxa, but distribution is defined as much by the area that a species does not occur as by where it occurs. False absences may lead to bad scientific decisions (Yoccoz et al. 2001, Buckland et al. 2011), and those decisions may lead to the waste of limited conservation resources. There are many methods for correcting for the detectability of individuals (Williams et al. 2002, Buckland et al. 2011), but they are usually too expensive to be applied in general surveys. In contrast, evaluation of the detectability of species may allow much better estimates of the proportion of the landscape occupied by a given taxon (MacKenzie et al. 2002).

Estimates of species detectability and occupancy generally require repeated surveys of sampling units, though in some cases space can be substituted for time. To be able to use those techniques, it is important that detailed information is available about where organisms were collected, and the effort expended to detect them. This is relatively easy to do with the spatially standardized sampling units used in the RAPELD system. Precise coordinates are often available for specimens collected in conventional surveys, but researchers who do not collect in spatially standardized units usually do not report sampling effort, especially if no specimen was collected. Spatially standardized units have allowed the evaluation of occupancy in RAPELD modules, and will allow long-term changes in occupancy to be evaluated. Even in the case that the researcher is confident that they record all the species within a sampling unit (a rare occurrence in the field, but common in researcher imaginations), quantifying detectability greatly increases the confidence that other researchers and managers will have in the results.

Uncertainty about complementarity

Complementarity is a core concept in systematic conservation planning (Jost et al. 2011, Kukkala and Moilanen 2013). However, most of the software used assumes that there is complete knowledge of the distribution of species, and this is not the case for many bio-diverse taxa in bio-diverse regions (see sections on detectability and distributions above). Studies by Ana Albernaz in the Alter do Chaõ region showed that, when these assumptions are not met, results reflect more the distribution of sampling than the distribution of the biota (Magnusson et al. 2013).

There are other options for planning, such as the use of complementarity of species assemblages based on multivariate ordination techniques (e.g. Reyers et al. 2002, Ilg et al. 2012) and selection of sites for additional sampling when initial sampling is inadequate (e.g. Lin et al. 2008). However, spatially standardized sampling is generally the easiest option to evaluate the assumptions of analyses, and standardized sampling has allowed evaluation of the effects of scale and position of sampling units in RAPELD plots (Franklin et al. 2013) and elsewhere (Chisholm et al. 2013).

Uncertainty about data quality and management

For monitoring, data is generally a more important product than scientific publications (Costello et al. 2013, Piwowar 2013). There are many schemes for storing and making data available, often with automatic upload by individual researchers. However, just having the system available does not mean that it will be used, leading to the "empty archive" syndrome (Nelson 2009). Also, data with errors may be worse than no data at all. We were unable to achieve adequate data quality just by offering information-technology resources; we had to have a human in the system (Pezzini et al. 2012, Magnusson et al. 2013). Other organizations have come to the same conclusion (Billick 2010). The spatially standardized system facilitated the production of data forms, but the flexibility in the taxa and collecting techniques added to the complexity of the process.

We were initially uncertain as to the best way to make data available. There are many database programs available, and information-technology specialists are always willing to develop another one. However, use of a single database for all the data is not viable for diverse monitoring data (Hale 1999), and it is more efficient to use a data repository that can be used to populate different databases with different purposes (Reichman et al. 2011). In this case, searches are undertaken on the metadata rather than the data themselves (Evans and Foster 2011). In the end, we found that the technology available far exceeds the ability of researchers to use it.

The information-technology revolution is recent, and none of our major field researchers had formal training in data management. Worse still, most university programs still do not offer specific courses in the principles of data management to biologists, though some do offer courses in the use of specific database programs. Data management is not easy or intuitive, and it is a critical phase in research that can effectively nullify all the planning that has gone into data collection. In the end, we found that the major uncertainties were related to whether (1) researchers would be motivated to make their data available, (2) whether researchers had already lost critical data in the field, (3) whether researchers had sufficient training to effectively deposit data, and (4) whether we could find the resources to undertake the capacity building and data verification necessary. Every major project should have a full time data manager responsible for training and data screening, but few do.

We adopted the Ecological Metadata Language (EML) used in the Metacat system (Fegraus et al. 2005) by the International Long-Term Ecological Research (ILTER) sites. However, we found that the generic coordinates required by that system, which basically just locate the study site, were not sufficient for most ecological analyses, especially of local landscapes. As the sampling sites are standardized, it was relatively easy for us to annex accessory metadata tables <http://ppbio.inpa.gov.br/sites/default/files/repositorio_PPBio_maio_2012.rar> to the EML metadata so that researchers could easily record the detailed information that will make their data useful to the broadest range of researchers in the future.

Conclusions

I have covered only a few of the sources of uncertainty that a field monitoring scheme has to deal with, but they illustrate the complexity of the problem. We are monitoring because we are uncertain, so uncertainty has to be a central issue in any monitoring scheme. However, biodiversity monitoring is more complex than monitoring physical phenomena, such as weather, because there are so many definitions of biodiversity, and it has different values for different segments of society (see Haila et al. 2014).

When we first implemented RAPELD, we opted for a hierarchical design, with regular sampling at the local level, but sampling sites limited by logistical considerations over larger areas. Although there was little theoretical support for it at the time, it has been useful to respond to a wide range of questions of interest to decision makers (Magnusson et al. 2013), it is similar to designs adopted by other researchers faced with sampling biodiversity over large areas (e.g. McDonald 2012, Olsen et al. 2012), and it is a design that has since been approved by experienced modelers for continent-wide monitoring (e.g. Franklin 2009, Johnson 2012, Reynolds 2012). Because the design is modular, it can be adapted to a wide range of situations. At first, we envisaged that most sites would have 5 km × 5 m grids, but the most favored module today is 5 km × 1 km. We were uncertain about everything and adopted a learning-by-doing approach, while always trying to maximize comparability with data collected previously. We are more surprised at how little we have had to modify the original design than by the changes we have implemented (Magnusson et al. 2013).

We were even uncertain about the questions that researchers will want to answer in the future using the data we are collecting today. Therefore, rather than adopting a taxon- or question-oriented approach, we focused on a spatial design that allows flexibility in questions and taxa studied, while allowing the landscape-geographical approaches required by conservation biology. It is a compromise, but a necessary one. RAPELD sites are being used to answer many specific questions, so the trade-off is generally not between monitoring and answering specific questions. It is between investing in field infrastructure and planning now, rather than in short-term studies that are good for researcher curricula, but that contribute little to long-term, wide-scale conservation planning. At the moment, many citizen monitoring programs, combined with good data availability, are contributing more to our understanding of global phenomena, such as climate change, than are more scientific programs (Schmeller et al. 2009), despite criticisms from academics (e.g. Ferraz et al. 2008). We professional scientists need to learn from the amateurs, and incorporate planning, standardization, and data availability, while maintaining the flexibility that uncertainty demands.

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Towards a different attitude to uncertainty

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Abstract

The ecological literature deals with uncertainty primarily from the perspective of how to reduce it to acceptable levels. However, the current rapid and ubiquitous environmental changes, as well as anticipated rates of change, pose novel conditions and complex dynamics due to which many sources of uncertainty are difficult or even impossible to reduce. These include both uncertainty in knowledge (epistemic uncertainty) and societal responses to it. Under these conditions, an increasing number of studies ask how one can deal with uncertainty as it is. Here, we explore the question how to adopt an overall alternative attitude to uncertainty, which accepts or even embraces it. First, we show that seeking to reduce uncertainty may be counterproductive under some circumstances. It may yield overconfidence, ignoring early warning signs, policy- and societal stagnation, or irresponsible behaviour if personal certainty is offered by externalization of environmental costs. We then demonstrate that uncertainty can have positive impacts by driving improvements in knowledge, promoting cautious action, contributing to keeping societies flexible and adaptable, enhancing awareness, support and involvement of the public in nature conservation, and enhancing cooperation and communication. We discuss the risks of employing a certainty paradigm on uncertain knowledge, the potential benefits of adopting an alternative attitude to uncertainty, and the need to implement such an attitude across scales – from adaptive management at the local scale, to the evolving Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) at the global level.

Keywords

Biodiversity conservation, communication, externalization, adaptive management, risk management, policy inaction, science-policy dialogue, IPBES

Introduction

The rapid growth in human population, combined with a steep increase in resource- and energy-demands, exert unprecedented pressures on Earth's natural resources (Rockstrom et al. 2009). Natural and semi-natural habitats continue being rapidly converted or degraded in response to humanity's growing needs. These rapid changes raise uncertainties about the future of biodiversity, ecosystem functioning and services. Additional sources of uncertainty emerge from rapid social, economic, political, and technological changes (to name just a few). The conservation of biodiversity is thus subject to an exceptional range of challenges and sources of uncertainty.

The topic of uncertainty in biodiversity research and conservation practice has traditionally focused on the realms of knowledge, also referred to as epistemic uncertainty (Regan et al. 2002). The literature often focuses on three main origins of such uncertainty: i) data, ii) models and iii) predictions - as well as their propagation along the scientific process (e.g. Regan et al. 2002; Burgman et al. 2005; Sutherland 2006; McDonald-Madden et al. 2010; Conroy et al. 2011; Polasky et al. 2011; Beale and Lennon 2012; Evans 2012). Important distinctions were made between imperfect knowledge (Funtowicz and Ravetz 1991) and inherent, or ontological uncertainty, due to stochasticity or randomness (Regan et al. 2002; Evans 2012; Haila and Henle 2014). Yet, the literature is very limited in consideration of other sources of uncertainty (Funtowicz and Ravetz 1991; Regan et al. 2002; Smith 2007; Mitchell 2009; Haila and Henle 2014). Particularly, sources of uncertainty pertaining to the "societal sphere" (as opposed to the "knowledge sphere") have received little attention. They emerge as soon as knowledge has to be transferred, translated, shared, and implemented in the decision-making process (Ibisch et al. 2012). For instance, linguistic uncertainty emerging from vagueness and ambiguity can add confusion independently of epistemic uncertainty (Regan et al. 2002). Additionally, uncertainty may originate from societal response, ranging from social vindication to public consent, scepticism, or rejection.

It is important to realize that all dimensions of uncertainty strongly interact: subjective judgements surrounding the knowledge sphere are shaped by uncertainty levels belonging to cognitive processes (i.e. pre-conceptual (data), conceptual (proxy) or symbolic levels (concepts) (Gärdenfors 2004; Haila and Henle 2014)). Ultimately, uncertainty arising from the societal context affects decision-making (Marzetti and Scazzieri 2011), and human preferences or fickleness create complex feedbacks among the components of socio-ecological systems (Levin 1999; Francis and Goodman 2010).

Traditional approaches focusing mostly on reducing (epistemic) uncertainty, e.g. through narrowing it within frequencies and quantity intervals or gathering further evidence, are likely to be insufficient (Sutherland 2006; Conroy et al. 2011; Evans 2012). Besides, some aspects of uncertainty remain intrinsically irreducible (e.g. "unknowables"; Ibisch et al. 2012). Discussions conducted within two workshops on the topic of uncertainty in biodiversity conservation, held in November and December 2011 in Leipzig, Germany, identified three alternative approaches to dealing with uncertainty: reducing it, accepting it, or embracing it (Haila et al. 2014). In accordance with these discussions, here we seek to explore how accepting and embracing uncertainty can promote progress in biodiversity research and conservation practice. While some recent studies addressing uncertainty in ecology have called for accepting the limits of knowledge and the realms of non-knowledge (Beale and Lennon 2012; Ibisch et al. 2012), this paper attempts to break the unspoken assumption that "certainty is good" while "uncertainty is bad". To this end, we first illustrate cases where seeking certainty may have undesired effects. We then exemplify circumstances where uncertainty, or the attitude to it, can yield positive outcomes. Our subjectively collected examples do not attempt to provide a comprehensive coverage of the literature, but rather aim to facilitate a constructive discussion toward a new and more flexible attitude toward uncertainty. Not all examples come from the biodiversity conservation realm, but we believe that all of them have relevant implications for this field.

Perverse effects of seeking certainty

A main problem with uncertainty may be the exaggerated pursuit of certainty. Seeking certainty can pervade knowledge gathering and use, potentially leading to overconfidence, ignoring the uncertain, stagnation or inaction while awaiting stronger evidence and irresponsible behaviours originating from the seeming certainty offered by externalizing the environmental consequences of our actions. In the following, we elaborate on each of these circumstances.

Overconfidence

Overconfidence can be defined as using incomplete knowledge as if it was absolute truth. To exemplify how overconfidence relates to uncertainty, we focus on the use of simplified metrics (e.g. threshold values) for ensuring species' viability under anthropogenic pressure, or maintaining the sustainability of utilized natural resources. Identifying such thresholds is achived through a long cognitive process of simplification, including the use of models. For instance, Population Viability Analyses (PVAs) are commonly used to identify critical thresholds below which populations would collapse. PVAs employ models ranging from simple mathematical or statistical formulations, to complex, parameter-rich, individual-based models. Model outputs are then aggregated to deliver understandable and digestible (but decisive) information for decision makers, while often evicting the communication of model details, assumptions, limitations, and associated uncertainties. Policy-makers may continue the chain of simplification, e.g. by utilizing even simpler measures as elaborated below.

A first example is the concept of Minimum Viable Population size (MVP) under which populations are assumed to be non-viable. Factors affecting this value for a given species include taxonomy, life history or environmental conditions (Flather et al. 2011), yet the demand for simple rules of thumb have led some ecologists to propose that populations (of any species) "require sizes to be at least 5000 adult individuals" (Traill et al. 2007). The use of such 'magic numbers' can be misleading or even wrong (Flather et al. 2011). Another important metric is the Minimum Area Requirement (MAR), defining the minimum habitat area for a viable population. While offering policy-relevant information, especially for spatial planning, it is notable that alternative scenarios, explored within a given study, may offer MAR values differing by as much as two orders of magnitude for the same species and site (Pe'er et al. 2014b). Under such uncertainty, the MAR values finally communicated to stakeholders may reflect primarily subjective decisions.

The third example is the Maximum Sustainable Yield (MSY), which defines the largest yield (or catch) that can be removed from a stock over an indefinite period without causing a population or species' collapse (UN 1997). MSY thresholds have been long criticised for being over-simplistic (Larkin 1977), especially in the fisheries context (Quaas et al. 2013). Yet for policy-support, even simpler metrics are used that focus merely on quotas, such as Individual Fishing Quotas (IFQs) or (trophy) hunting quotas. The application of these metrics is are known ti support overfishing, driving declines in population sizes and biomass, as well as evolutionary changes in harvested species (e.g. Coltman et al. 2003; Ernande et al. 2004; Palazy et al. 2011). Overfishing further leads to marine biodiversity declines (Ye et al. 2013) and potentially even ecosystem collapses (Richardson et al. 2009). Nonetheless, these metrics remain the general norm in hunting and fisheries' policies.

These examples illustrate widely used practices in biodiversity management, where trying to reduce uncertainty can generate overconfidence or misguidance. Simple and clear metrics might ease communication between scientists and decision-makers, but can lure judgement if inadequately designed or lacking sufficient information on wildlife populations (Flather et al. 2011). At times, these values reflect nothing but guesswork (Lindsey et al 2007). In addition, a range of uncertainties remain poorly considered or communicated (Pe'er et al. 2014b). Communicated values and confidence intervals are subject to judgment interpretation, often dictated by societal aspects: thresholds that are over-restrictive may be rejected by civil society or policymakers (Pe'er et al. 2014b), promote misreporting and thereby enhance uncertainty with respect to population status (Quaas et al. 2013), or are simply posing goals that are too challenging to meet (e.g. Palazy et al. 2011; Quaas et al. 2013). These examples therefore demonstrate the perverse outcomes of a demand on scientists to support policy by maximising the (seeming) certainty with respect to the recommendations provided to policymakers. This attitude dictates the use of over-simplified thresholds, offering overconfidence rather than a true characterisation of ecological knowledge and its limits.

Ignoring the uncertain

Seeking certainty at all costs can hinder knowledge seeking and distort its interpretation, thereby slowing down the learning process. It remains an implicit goal of scientific research to obtain 'perfect knowledge' of Earth's systems. To reach this goal, scientists simplify, transform, and aggregate evidence to identify and understand patterns and their underlying processes. Yet in the quest for understanding general patterns, the importance of outliers is often underestimated (Ibisch et al. 2012). Rare and extreme events may be exceptionally meaningful in revealing the capacities that individuals, species or ecosystems may exhibit. They are known to shape species distribution ranges and range shifts, as these are largely determined by rare long-distance dispersal events. Likewise, rapid evolutionary changes are proposed to occur during rare and rapid branching speciation events, known as "punctuated equilibrium" in evolutionary ecology (Gould and Eldredge 1993). However, because rare events are difficult to measure and analyse statistically, they remain under-explored. For instance, while PVAs frequently indicate that catastrophes and environmental stochasticity exert strong effects on simulation outcomes, a recent review could not detect an increase over time in the proportion of studies examining their effects, or the number of studies incorporating several concomitant sources of stochasticity (Pe'er et al. 2013a). PVAs therefore continue under-exploring, and likely underestimating, the impacts of rare, extreme or complex events.

Disregarding the unexpected can lead to 'black swan' situations where events that were considered highly improbable and irrelevant turn out to be both real and incurring significant impacts (Taleb 2008). In ecology, the risk of black swans emerges from the vast range of environmental processes that are either non-linear or complex, such as feedback loops leading to tipping-points (Richardson et al. 2009; Lenton 2011), extinction debt (Tilman et al. 1994) followed by a spiral of ecosystem impoverishment (Carpenter et al. 2006) or vortex of extinction (Gilpin and Soulé 1986). It is true that such processes remain difficult to analyse with current decision-making tools (Polasky et al. 2011), but compulsively targeting perfect knowledge may lead to neglecting critical evidence (Evans 2012), ignoring early warning signs, or underestimating the potential effects of such incidences (Ibisch et al. 2012). Such an attitude can further weaken the ability to reconsider current understanding, and can paradoxically support the preservation of imperfect knowledge.

Awaiting certainty as a driver of stagnation

Seeking complete certainty may delay action until strong(er) evidence can be obtained. In the meantime, however, habitat loss, fragmentation and degradation, as well as climate change, continue unabated. A prominent example of societal demand for greater certainty, accompanied by inaction, is represented by the debate over climate change, and the work of the Intergovernmental Panel on Climate Change (IPCC). Discussions over the last decades revolve primarily around two core questions: whether climate change is occurring (including speed and severity), and whether it is caused, or significantly facilitated, by anthropogenic factors such as greenhouse gas emissions (IPCC 2013). While there is by now general acceptance that global warming is taking place, the exact contribution of humans remains under debate. Combined with uncertainties around questions of governance and best actions – namely, who should do what (e.g. Ackerman and Finlayson 2006; Bosetti et al. 2009), societies and policymakers show great resistance to take an action. The Costs of Policy Inaction (COPI; Bakkes et al. 2007), however, is likely to increase over time.

While biodiversity is affected by various forms of policy inaction in the climate change context (IPCC 2002), an example for policy stagnation with more direct relevance to biodiversity loss is the recent reform of the Common Agricultural Policy (CAP) in the European Union. Following a complex negotiation process (Rutz et al. 2013), the CAP reform failed to offer effective measures to halt ongoing declines in farmland biodiversity (Pe'er et al. 2014a). The link between agricultural intensification and biodiversity loss is well established (MA 2005; EEA 2010, 2013), and there is also growing evidence that the benefits accrued from maintaining biodiversity exceed the inclusive, long-term and larger-scale costs of losing biodiversity and ecosystem services (TEEB 2010). However, farmers and the food industry can see short-term, measurable economic gains from intensifying agricultural productivity, whereas the monetary and societal costs incurred by biodiversity loss and ecosystem degradation are complex, poorly quantified or even unquantifiable (Pe'er et al. 2014a). Consequently, arguments in favour of biodiversity conservation were either weakened by uncertainty, or put aside in face of a stronger focus on food security and food production. Retaining the CAP largely unchanged (see Rutz et al. 2013) therefore offers a good example where policy stagnation emerges, at least in part, from a societal attitude that puts higher weight on certain, short term benefits than on long-term benefits (or costs) that are associated with higher uncertainty.

A third example of how the quest for certainty can lead to stagnation is the "cautionary silence", where experts may avoid engaging in a science-policy dialogue out of the fear of making seemingly-uninformed statements (Pe'er et al. 2013b). In the case of the Norwegian Nature Index, it was paradoxically the experts "… working with the most accurate and precise population data [who] were also the ones most reluctant to use their presumably excellent expert knowledge to extrapolate beyond their observations" (Haila et al. 2014).

Personal certainty allows ignoring negative environmental effects

Environmental externalities occur when an action produces environmental costs or benefits to a third party that was not involved in the action. Externalities can be spatial, affecting different locations or acting at a larger spatial scale; or temporal, i.e., acting at a different point in time and affecting, for instance, future generations. Prominent examples for negative externalities include air, water or soil pollution, which put a range of costs on humans and the environment, usually at larger scale than the actions of single individuals; or externalization of environmental costs to poorer societies (MA 2005).

In today's globalized world, where international trade chains often put large distances between production areas and consumers, environmental externalities often occur across continents (Lenzen et al. 2012). Displacement of land-use, where land-use changes emerge from consumption elsewhere, largely acts from high-income to low-income countries while putting pressure on ecosystems in the latter (Weinzettel et al. 2012). Lenzen et al. (2012) estimated that 30% of red-listed species are threatened due to internationally traded commodities like coffee, tea, sugar, textiles or fish. One might argue that end-consumers may not be aware of the negative environmental consequences of their action, partly due to complex causal relationships (Hertwich 2012). However, it can also be asserted that consumers often act under the assumption of "personal certainty" regarding their own security. Globalization of markets and externalization of environmental costs render consumers, especially in high-income countries, immune to the (immediate) consequences of their consumption attitudes. Resource shortage or price fluctuations can be easily buffered at the consumer level by shifting markets, but can generate poverty or local food-scarcity at the area of production, often located in low-income countries. The certainty that one's actions will not expose oneself to environmental or societal costs, thereby promotes unsustainable or even irresponsible behaviours.

A local scale example in which personal security can lead to unsustainable behaviour is risk avoidance offered by insurance. In dryland pastoral systems, where environmental uncertainty is an inherent property of the ecosystem, farmers historically developed approaches such as mobility, reliance on social networks for building up herds after catastrophic events, and setting aside open grasslands as grazing reserves for emergency times (Müller et al. 2011). Apart from their usefulness to deal with uncertainty (with respect to income), these strategies often have positive ecological and social by-effects. Nowadays, farmers can reduce their risks by contracting insurances, which compensate them in the case of reduced rainfalls below a certain level. Reducing the economic risks, however, replaces the necessity for ecosystem-based buffers. This potentially leads to a modification in farmers' behaviour, up to abandoning traditional sustainable strategies such as the protection of parts of the pasture in rainy years to use it as a reserve for dry years (Müller et al. 2011).

These examples demonstrate that, across scales, seeming certainty offered by externalizing environmental costs may promote irresponsibility or unsustainable practices – thus laying the foundations of the tragedy of the commons (Hardin 1968, Ostrom 1999, 2009).

Positive outcomes of uncertainty

In the following sections we offer illustrative examples of circumstances where uncertainty, or the attitude to it, can yield positive outcomes: driving improvements in knowledge, promoting cautious actions, enhancing a more flexible and adaptive societal behaviour, raising public awareness and engagement in nature conservation, enhancing cooperation, and promoting communication.

Driver for improving knowledge

Research is driven by the quest for improved understanding and certainty in knowledge. Yet one could also assert that science and scientists thrive on uncertainty: open questions make the world interesting and exciting, and motivate our quest for knowledge. Uncertainty not only guides the starting point of learning processes, but is also a key element at the closing of learning iterations. Descartes' "philosophy of the doubt", upon which science still greatly relies, does not build on removing uncertainty but rather on clearly identifying it en-route to so-called "perfect knowledge" (Descartes 1637). This entails identifying gaps, imprecision, inaccuracy, or any weakness associated with the process of understanding; excluding all questionable beliefs in the pursuit of scientific truth; and, at the end of any learning step, explicitly identifying and acknowledging the remaining uncertainty. Thereby, one obtains relevance and confidence in the outcomes of the scientific exploration, compared to leaving uncertainty inextricable.

Promoting caution in action

Uninformed decisions taken by policy-makers and decision-makers could result in long-term risks to humans, the environment, or both. Insufficient scientific evidence could, in such cases, promote cautious and responsible actions if a precautionary approach is taken (see also Haila et al. 2014). Specifically, the precautionary principle has the power to promote decisions on the basis of uncertainty itself: to this end, it is required to a) use currently available data, b) indicate uncertainty, c) identify potentially adverse effects and d) evaluate the potential consequences of inaction (EC 2000). The precautionary principle hence enables avoiding policy inaction when knowledge is insufficient. It explicitly adopts an attitude that accommodates uncertainty into decision making and "…enables rapid response in the face of a possible danger to human, animal or plant health…" (EC 2000). This principle is well established in the European Union's law, including the Habitats Directive, and was adopted by the Convention on Biological Diversity (CBD 2004). A particularly interesting examination of the precautionary principle in biodiversity conservation relates to ecological restoration: restored ecosystems might prevent or reduce the impacts of environmental catastrophes (Wiegleb et al. 2013). The precautionary principle hence demonstrates that an alternative attitude to uncertainty can promote both reactive and proactive conservation actions.

Promoting societal flexibility, responsiveness and adaptability

Social acceptance of unknowns may allow societies to stay attentive to early warning signs, and maintain sufficient conceptual and practical flexibility for an effective response. It may reduce the risks of disregarding "black swans", as societies may be better prepared to accept that the unexpected is likely to occur in a period of unforeseen, rapid changes. It may further allow quick adoption of alternative reaction paradigms, should current ones fail (Carpenter et al. 2006; Polasky et al. 2011). In conservation practice, an example of a more flexible decision-making process is the employment of adaptive management, defined as "an iterative decision-making process under uncertainty that is designed to learn and incorporate new information and thereby improve future decision-making" (Polasky et al. 2011). This approach views management decisions as experiments, whose impacts need to be tested, monitored and assessed within a "learning by doing" process (Keith et al. 2011; Westgate et al. 2013; Haila et al. 2014). Adaptive management can gain from embracing uncertainty, as this entails viewing learning in a positive light, and welcoming the opportunity to experiment.

Raising public awareness and engagement

Uncertainty can be used to call for conservation actions, with direct benefits for species as well as promoting public awareness and engagement. Particularly, risks of species' extinction often confront scientists and practitioners with a conflict known as "Noah's Arch dilemma": which species should we save first? (Scott and Csuti 1997; Higgins et al. 2004; Perry 2010). Different conservation schools suggest we should maximise the number of species to be protected (Wilson et al. 2011), safeguard irreplaceable ecological functions (Perry 2010), or seek to maximise cost-effectiveness of conservation efforts in light of uncertainty (Salomon et al. 2013). By contrast, translocations, reintroductions and assisted colonisations of focal threatened species are characterised by high costs and low chances of success. Nonetheless, they receive strong societal support and substantial investments (Fischer and Lindenmayer 2000; Armstrong and Seddon 2008). Such efforts face various uncertainties, due to limited knowledge, high stochasticity, and little room for mistakes. One can justify such efforts by ethical arguments, the importance of specific cultural services provided by such species (Mech 1995) or their key contribution to the functioning of ecosystems. Yet note that the appeal of such actions lies especially in spectacular success stories, where species were rescued from extinction from just a few remaining individuals. Some prominent examples are the Arabian Oryx (Stanley-Price 1989), Californian condor (Walters et al. 2010), Przewalski horse (Boyd and Houpt 1994), wisent (Tudge 1992) and Persian Fellow deer (Bar-David et al. 2005).

The relation of such successes to uncertainty can be viewed in two ways. First, on the choice between uncertain chances to save a species versus high risk of extinction if no action is taken, the choice for uncertainty is a choice for hope. Secondly, the natural uncertainty around such emergency actions, and the ambition behind them, help raising public attention, awareness and engagement, and attracts important funding to nature conservation. Hence, uncertainty can be an important driver of action in situations where inaction could lead to irreversible, undesired losses.

A driver of cooperation

Uncertainty can enhance, or even drive, cooperation among animals and humans alike. Theories on the evolution of sociality have long suggested that resource scarcity or unpredictability, or enhanced risks for individuals, can be key drivers toward cooperation (Cohen 1966; Lin and Michener 1972; Frank and Slatkin 1990; Jetz and Rubinstein 2011). While some recent studies demonstrated that resource scarcity or unpredictability (e.g. in relation to climate change) can enhance conflicts and violence among humans (Le Billon 2001; Hsiang et al. 2013), other, less prominent studies point out that resource variability can also promote cooperation (Bogale and Korf 2007; McAllister et al. 2011). An interesting example on the emergence of cooperation examined local versus large-scale social conflicts originating from heterogeneity in wealth and resources (Abou Chakra and Traulsen 2014). This study examined social dilemmas with tension between individual incentives to optimize personal gain versus social benefits. An additional cause of conflict was the uneven allocation of resources between rich and poor. Using a simulation model which assumes a collective-risk dilemma, Abou Chakra and Traulsen (2014) found that enhanced uncertainty may lead to increased cooperation where the rich assist the poor. However, the poor contributed only when early contributions were made by the rich players. This study therefore points out that uncertainty can indeed lead to cooperation, even at large scales, but this requires that relevant players acknowledge their responsibility for this to happen. This example warrants attention in the context of the global biodiversity crisis, because global hotspots of biodiversity and its loss are concentrated especially in low-income countries (Myers et al. 2000).

Promoting communication and trust

In the scientific world, explicit consideration of limitations promotes credibility when communicating knowledge. In the same way that a scientific paper gains credibility by explicitly discussing its limitations, scientists communicating their knowledge to the public are anticipated to exhibit honesty with respect to uncertainty. This is well exemplified through the "ClimateGate" event: internal discussions over uncertainty, which were not communicated transparently, have eased the case for those seeking to distrust the work of the IPCC (van der Sluijs et al. 2010; Ravetz 2011; Garud et al. 2014). Ravetz (2011) suggested three main take-home messages from this incident: "1) quantify uncertainty, 2) building scientific consensus […and retain] 3) openness about ignorance". Garud et al. (2014) suggested that the tension between "normal science" - as perceived by scientists - and "post-normal science" constellations, where high stakes meet high uncertainty, requires an alternative approach altogether. Accordingly, the fourth assessment of IPCC has indeed adopted a new approach to uncertainty, where comments are documented and dealt with in a completely transparent way (IPCC 2013).

Discussion

Using some illustrative examples, we have shown that seeking to reduce uncertainty by all means can produce a range of adverse outcomes, including oversimplification and overconfidence, or policy stagnation due to awaiting greater certainty. On the other hand, accepting and embracing uncertainty can have positive impacts such as favouring cautionary actions, flexible solutions, greater cooperation and transparent communication.

As our focus is biodiversity conservation, many examples focus on conflicts between humans and nature, and involve uncertainties originating from the complexity of integrating the interests of multiple actors. While predictive ecology continues to evolve towards better understanding of such dynamic processes (Evans 2012), our understanding of socio-ecological systems is only starting to develop, and the field retains, and will likely continue retaining, large degrees of unpredictability (Walker and Salt 2006; Scheffer et al. 2009; Polasky et al. 2011).

A range of novel approaches can now integrate multiple sources of uncertainty, offering promising frameworks to aid policy-makers and practitioners in defining effective strategies and solutions under uncertainty. These include decision theory and scenario-planning (reviewed by Polasky et al. 2011; Grechi et al. 2014; Knights et al. 2014), as well as the approaches proposed within the realms of post-normal science (Ravetz 2004; Francis and Goodman 2010).

Notwithstanding, biodiversity research still focuses primarily on reducing Type 1 errors: failing to reject a wrong hypothesis (Schneider 2006). This entails a strong preference for reducing uncertainty. Decision makers, by contrast, are usually more concerned about committing Type 2 errors, namely, rejecting a correct hypothesis (Schneider 2006), probably because their governance responsibilities make them more prone to avoid taking decision only if risks might exceed acceptable thresholds. This creates a dichotomy where scientists may adopt a "precautionary silence" while awaiting better evidence, whereas policy-makers continue taking decisions within a "business as usual" framework. Such dynamics maintain or even increase the pressures on biodiversity. We therefore assert that the dominating certainty paradigm brings researchers, practitioners, decision-makers and the public alike to share the common assumption that ecological research can, and should, support policy by seeking to reduce uncertainty. Thereby, we maintain overconfidence and policy stagnation, discard of early-warning signs, or adopt irresponsible behaviours. We see this attitude as unnecessary because policymakers are surely aware of, and obviously accept, uncertainty in other fields. For example, economic decisions and negotiation processes not only incorporate and accept uncertainty, but often even maintain it deliberately in order to allow some freedom in interpretation or implementation. An alternative is therefore to enhance the acceptance, by all parties, that biodiversity research and conservation act largely in the realms of uncertainty. We do not perceive such an alternative attitude as a replacement to the quest for knowledge and certainty, but as an expansion of the range of potential responses to uncertain conditions.

Implications across scales

The need for a new attitude to uncertainty can be demonstrated across scales, from local to global. Locally, adaptive management is already mentioned by thousands of ecological studies, yet surprisingly few really adopt this principle, and even fewer can show documented successes (Westgate et al. 2013). Among the key reasons are insufficient monitoring, and insufficient addressing of social aspects (Westgate et al. 2013). These challenges indicate that, for adaptive management to become successful, a change in attitude to uncertainty is needed among all parties.

At larger scales, the precautionary principle has only rarely been successfully applied in biodiversity conservation, partly due to the lack of sufficient guidance to move from awareness to implementation (Tisdell 2011; Kanongdate et al. 2012; Rayfuse 2012). Greater acceptance of uncertainty and its implications would likely reduce the risk of societal resistance if the principle is used.

Global efforts to understand and address the biodiversity crisis, especially through the evolving Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), need to tackle key questions on how to scale up ecological processes, pressures and solutions from local to global. Scaling up, however, entails propagation of uncertainty. Standing issues include the relationship between biodiversity and ecosystem services (Balvanera et al. 2014); the multitude of drivers acting across scales (MA 2005; Tzanopoulos et al. 2013); complex production-consumption chains (Hertwich 2012; Lenzen et al. 2012); and rapid political and socioeconomic changes, within which responsibilities need to be identified and decisions made. How IPBES will accommodate uncertainty in its decision making processes, thus remains an open and important question to resolve (Koetz et al. 2012; Pe'er et al. 2013b; Balvanera et al. 2014).

Developing an alternative attitude to uncertainty could start among scientists, acknowledging and communicating that the field of biodiversity research largely lies in the realms of uncertainty and therefore the demand for high confidence cannot always be fulfilled. Yet the fix of environmental decision-making on confidence intervals and significance levels, cannot be broken by scientists alone: it requires that stakeholders learn to accept a diversity of knowledge and non-knowledge inputs into the science-policy and science-society dialogue. In the process, the nature of the dialogue itself may change.

A cautionary point

While the main goal of this paper is to promote a broader range of attitudes to uncertainty, we do not wish to suggest that uncertainty should be always perceived as positive or welcome. There are numerous cases where uncertainty is clearly undesired, both in terms of associated risks and negative societal responses to it. A particular reason for caution should be given to circumstances where stakeholders or parties benefit from uncertainty or use it to achieve own goals. While in biodiversity conservation research we are only starting to understand the different aspects of uncertainty, other fields, e.g. economics, politics, or insurance, have gained far more experience in this area. Thus, how we deal with (and communicate) uncertainty may need caution depending on circumstances and parties involved. However, there are plenty of opportunities for learning.

Outlook

This paper focused on subjectively-collected examples to bring about a specific opinion. While we did not attempt to offer a comprehensive coverage of such cases, we recognize a need for an extended review. Elements of such a review would include mapping circumstances in which certainty, versus uncertainty, may promote or impede effective management of natural resources. A meta-analysis or quantification of the impacts could thus direct a better "choice of attitude" towards different forms of uncertainty.

To make these alternative attitudes operational in biodiversity conservation, it could also be desirable to examine attitudes toward uncertainty within legislative or judiciary frameworks in different parts of the world. For instance, it is worthy to explore differences between the European Union and the United States of America in terms of evidence-provision in court (i.e. respectively inquisitorial vs adversarial (Froeb and Kobayashi 2001)), or compare the precautionary principle, which is generally adopted by the EU, against the "burden of proof" approach applied in North America. The way uncertainty affects legislative systems may reflect the general attitude of societies to it. Better understanding of this relation may aid in developing operational alternatives in biodiversity practice.

Finally, we call for stronger trans-disciplinary research on the feedbacks between societal and scientific components in decision-making – e.g. in terms of "cost effective" or "best" conservation efforts given societal perception of "success". While we did not explore in depth any economic criteria for decision-making, one should acknowledge that it is primarily in economy that multi-dimensional approaches are adopted to address multiple sources of uncertainty. These are already increasingly adopted in ecological decisions in consideration of the societal sphere (Schneider et al. 2000; Polasky et al. 2011), as well as in analyses of trade-offs between competing decisions under uncertainty (Chee 2004; Stewart and Possingham 2005; Carwardine et al. 2010; TEEB 2010). Building on the experience gained through such studies, an iterative feedback process could be achieved between facilitating the development of alternative attitudes towards uncertainty, and integrating them into the science-policy dialogue.

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