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Referenties voor bodemecosystemen: evaluatie van functies en ecologische diensten

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RAPPORT IN HET KORT

Referenties voor bodemecosystemen: evaluatie van functies en ecologische diensten

Het bodembeleid gaat zich richten op een bewuster en meer duurzaam gebruik van de bodem, waarbij zowel de ecologische, economische als sociale dimensies meewegen. Dit is de boodschap die in de Beleidsbrief Bodem is verwoord die in december 2003 naar de Tweede Kamer is verzonden. In dit document wordt het raamwerk voor het bepalen van de duurzaamheid van het bodemgebruik voor wat betreft de ecologische dimensie –en de bodembiodiversiteit– verder ontwikkeld. In het rapport worden beschrijvingen van verschillende graslanden gepresenteerd (met name twee veehouderijbedrijven op zand en op rivierklei). Op basis van het actuele bodembeheer en ecologische theorieën, kunnen deze beschrijvingen beschouwd worden als referentiebeelden voor bodemecosystemen met een duurzaam bodemgebruik. Hier wordt een berekeningswijze geformuleerd, gebruik makend van gegevens uit veldobservaties en ecologische inzichten, om te verklaren hoe alle ondergrondse organismen beïnvloed worden door abiotische omstandigheden en beheer. De resultaten worden besproken met het oog op het definiëren van ‘kritische’ grenzen voor duurzame ecosystemen in landbouwgronden. De aanpak kan dan in de toekomst gebruikt worden om referenties voor andere bodemecosystemen te formuleren.

Trefwoorden: Allometrische relaties; Bodemvoedselweb; Gemiddeld lichaamsgewicht; *Nematode Channel Ratio*; Numerieke dichtheid van bodemorganismen

ABSTRACT

Reference assemblages for soil ecosystems: evaluating functions and ecological services

The Dutch soil policy is being focussed towards a more conscious and sustainable use of the soil, taking into account ecological, economical, and societal dimensions, as stated in the so-called ‘*Beleidsbrief Bodem’* sent to the Parliament in December 2003. In the present report the framework for the determination of the sustainability of land-use as far as the ecological dimension –and soil biodiversity– are concerned is described. On the basis of a large database containing soil biological monitoring data and on the basis of ecological models for soil food-web stability, we derived two reference soil ecosystems indicating sustainable land-use, i.e. one for diary farming on sand and one for diary farming on river clay. Using mathematical evidence derived from field studies, a hypothesis is formulated to explain how soil organisms become affected by increasing effects of land management. This is discussed in relation to defining ‘critical’ conditions for ecosystem sustainability in agricultural soils: only within such stable assemblages, in fact, a host of soil organisms may interact in ways beneficial to each other. The approach provides a useful tool to assess land-use quality in the future.

Keywords: Allometric relationships; Average body mass; Detrital food-web; Nematode Channel Ratio; Numerical abundance of soil organisms

Voorwoord

Het bodembeleid richt zich in toenemende mate op het duurzaam gebruik van de bodem. Dit is een breuk met het verleden, waar het beleid zich met name gericht heeft op de bescherming van de bodemkwaliteit. Bij gebruik van de bodem valt te denken aan ruimte om op of in te bouwen, maar ook aan de ecologische diensten die het bodemecosysteem levert om het bodemgebruik mogelijk te maken. Ecologische diensten (of nutsfuncties) omvatten de omzetting van organische stof, vorming van een goede bodemstructuur, het reinigend vermogen, de levering van schoon grond- en drinkwater, de onderdrukking van ziekten en plagen in de landbouw, etc. Deze nutsfuncties worden voor een groot deel door organismen in de bodem verzorgd en zijn van levensbelang voor de instandhouding van de kwaliteit van de omgeving en duurzaam bodemgebruik.

Duurzaam gebruik van de bodem houdt in dat de voortgang van de nutsfuncties op de lange termijn verzekerd moet zijn. Het rapport is opgebouwd uit twee delen, namelijk:

- een deel in het Nederlands met een zogenaamde ‘oplegnotitie’ en een achtergronddocument. Hierin worden achtereenvolgens gepresenteerd:
  - een uitleg over het raamwerk voor duurzaam bodemgebruik,
  - de blauwdruk voor de beantwoording van de beleidsvragen voor duurzaam bodemgebruik,
  - een uiteenzetting van de koppeling tussen nutsfuncties enerzijds~~,~~ en de bodem als levend systeem anderzijds,
  - de afleiding van referentiebeelden voor bodemecosystemen, inclusief twee voorbeelden.
- een deel in het Engels waar de wetenschappelijke verantwoording van de allometrische afleiding van ‘referenties’ in graslanden op zand en op rivierklei wordt onderbouwd. Daarnaast is het uitgebreide bestand met meetgegevens van de Bodembiologische Indicator (BoBI) geraadpleegd.

In dit rapport wordt een analyse uitgevoerd van verschillende modellen waarmee de stabiliteit van bodemecosystemen kan worden geschat. Op basis van deze modellen en de BoBI-meetgegevens is een optimale (lees: duurzame) samenstelling van de twee gepresenteerde bodemecosystemen beschreven. Deze set kan als ‘referentiebeeld’ gebruikt worden van duurzaam bodemgebruik.

Summary

The Dutch soil policy is being focussed towards a more conscious and sustainable use of the soil, taking into account ecological, economical, and societal dimensions, as stated in the so-called "*Beleidsbrief Bodem*" sent to the Parliament in December 2003. In the present report the framework for the determination of the sustainability of land-use as far as the ecological dimension and soil biodiversity are concerned is described. The framework departs from relations between land-use, ecological services, the soil as a living system, data on biological, chemical and physical characteristics, and the kind of soil management (application of nutrients, groundwater level, etc.).

On the basis of a large database containing soil biological monitoring data and on the basis of ecological models for soil food web stability, we derived two reference soil ecosystems indicating sustainable land-use, i.e. one for diary farming on sand and one for diary farming on river clay. This report is composed of two parts:

- A part in Dutch with a "memorandum" and a background document containing:
- An explanation of the framework on sustainable soil use;
- The scheme for the answering of policy questions on sustainable soil use;
- An explanation of the relations between ecological services on the one hand and the soil as a living system on the other hand;

- A part in English with the scientific justification of the chosen approach. Using mathematical evidence derived from field studies, a hypothesis is formulated to explain how soil organisms become affected by increasing effects of land management. This is discussed in relation to defining "critical" conditions for ecosystem sustainability in agricultural soils: only within such stable assemblages, in fact, a host of soil organisms may interact in ways beneficial to each other.

Inhoud

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1. Oplegnotitie

In de Beleidsbrief Bodem die in december 2003 naar de Tweede Kamer is verstuurd, staat beschreven dat de bodem als een dynamisch systeem beschouwd wordt: "*De bodem heeft een economische, sociale en een ecologische dimensie. Het ecologisch functioneren zal worden beoordeeld op basis van chemische, fysische en biologische parameters. De bodem wordt niet langer beschouwd als een statisch compartiment maar als een dynamisch ecosysteem.*" Het bodembeleid gaat zich richten op een bewuster, en meer duurzaam gebruik van de bodem, waarbij zowel de ecologische, economische als sociale dimensies meewegen.

De beleidsvragen die voortvloeien uit de nieuwe ontwikkelingen bij het bodembeleid richten zich onder meer op de beantwoording van vragen over de ecologische kwaliteit van de bodem, en hoe de bodem duurzaam gebruikt en verbeterd kan worden. Deze vragen spelen op alle schaalniveaus. Op lokaal niveau zal de gebruiker van de bodem (bijvoorbeeld een boer) geïnteresseerd zijn in de bodemkwaliteit van zijn percelen of terreinen en in de invloed van het bodembeheer daarop (bijvoorbeeld de hoeveelheid en kwaliteit van de bemesting). Op nationaal niveau is van belang of de Nederlandse bodem op de lange termijn zijn gebruikswaarde behoudt, of de ecologische gebruiksfunctie voldoende tot zijn recht komt, en welke invloed de ruimtelijke verdeling van de intensiteit en het type bodemgebruik daarop heeft.

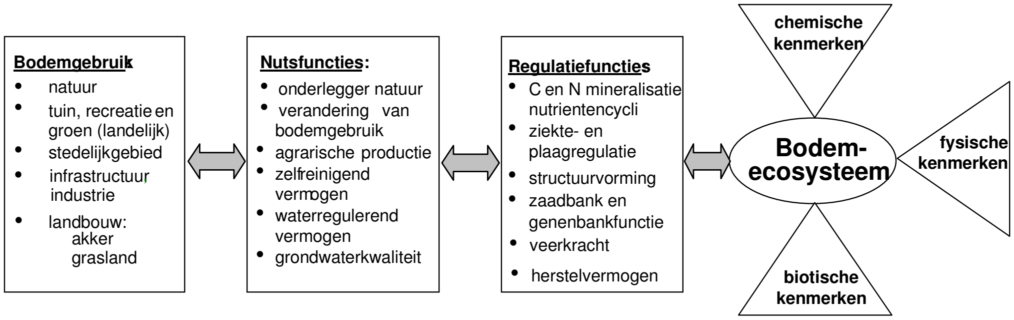
Het nieuwe bodembeleid houdt een zogenaamde 'kanteling' in. Tot op heden werd het beleid met name gericht op de belangrijke milieuthema's afzonderlijk. Voor de bodem was verontreiniging een belangrijk aandachtspunt, maar ook op het gebied van bijvoorbeeld verzuring en vermesting werd milieubeleid ontwikkeld. Het resultaat is een caleidoscopisch geheel van beleidsinstrumenten, waarin onvoldoende samenhang aangebracht kan worden om de bodem als samenhangend milieucompartiment op de lange termijn te beschermen. Er is behoefte aan een beleids- en beheersinstrument dat al het menselijk handelen en alle menselijke invloeden op de bodem integreert, en dat inzicht verschaft in de duurzaamheid van het bodemgebruik. Tevens dienen de gevolgen van verandering van beheer in beeld te worden gebracht.

Ook de aan het beleid ten grondslag liggende kennisontwikkeling dient gekanteld te worden. Beleidsrelevant onderzoek was met name gericht op de afzonderlijke effecten van specifieke milieufactoren op de bodemkwaliteit. Om deze kennis ook in de toekomst te benutten dienen de verschillende kennisvelden geïntegreerd te worden via een systeembenadering en zal er meer aandacht moeten komen voor de ecologische gebruiksfuncties van de bodem.

1.1 Maatschappelijke diensten

Een gezonde en levende bodem levert maatschappelijke diensten, de zogenaamde nutsfuncties. Deze liggen verankerd in het bodemgebruik (Figuur 1). Bij duurzaam bodemgebruik dient de gezondheid van de bodem optimaal in stand te worden gehouden, zodat de nutsfuncties ook op de lange termijn geborgd zijn. Het raamwerk wat hiervoor is opgesteld gaat uit van koppelingen tussen het bodemgebruik, de nutsfuncties, de bodem als dynamisch en levend systeem en de gecombineerde bodemkenmerken (biologisch, chemisch en fysisch) en omgevingsfactoren.

Om aan het streven naar duurzaam bodemgebruik invulling te geven zijn er kwaliteitsbeelden voor gezonde en niet gezonde bodem nodig, op basis van de systeembenadering in Figuur 1. Er is een grote variatie aan bodems als gevolg van variaties in bodemtype, en vormen en intensiteit van het bodemgebruik. Verwacht mag worden dat ook de gezondheid van bodems in Nederland sterk uiteen zal lopen. Voor de ontwikkeling van beleid voor duurzaam bodemgebruik is een beperkt onderscheid tussen bodemtypen en vormen van bodemgebruik onontbeerlijk. Afhankelijk van specifieke vragen zal dit in bepaalde gevallen nog verder gedetailleerd moeten worden bijvoorbeeld bij optimalisering van lokaal bodembeheer.



Figuur 1. Schematische koppeling tussen bodemgebruik en bodemecosystemen op basis van de maatschappelijke diensten (nutsfuncties).

Uitgaande van het bodemgebruik worden nutsfuncties van het bodemecosysteem gedefinieerd. De nutsfuncties zijn vervolgens te herleiden tot de regulatiefuncties als onderdeel van een levende bodem. Het bodemecosysteem kan worden vastgelegd op basis van biologische, chemische en fysische kenmerken. Biologische kenmerken zijn bijvoorbeeld biomassa, biodiversiteit, mineralisatie processen, voedselwebkarakteristieken en dynamiek.

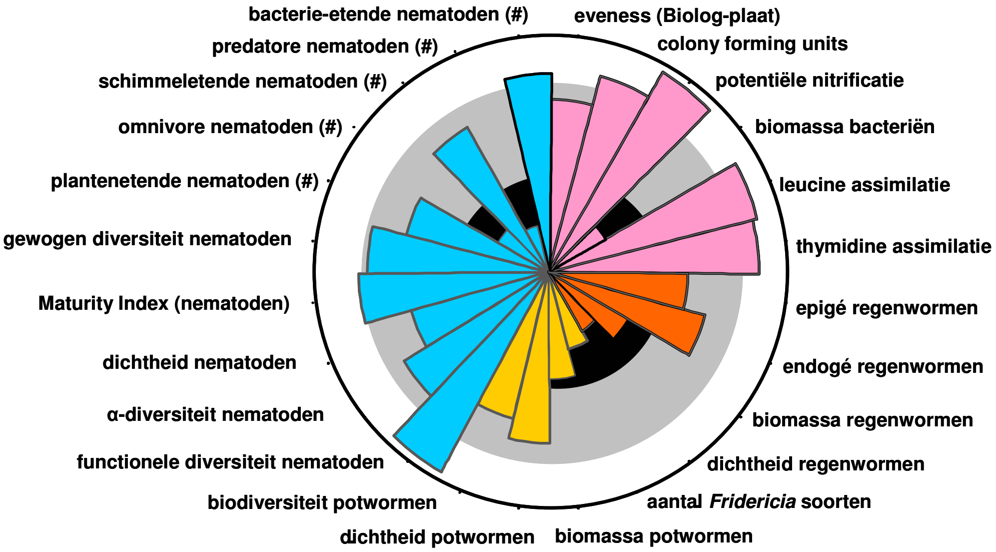
1.2 Referentie- en kwaliteitsbeelden

Er is de afgelopen jaren gewerkt aan de ontwikkeling van een instrumentarium om op een gestandaardiseerde wijze bodemparameters te meten die van belang zijn voor de bepaling van de gezondheid van de bodem, de zogenaamde Bodembiologische Indicator (BoBI). Op het vlak van chemische en fysische indicatoren is ruime ervaring en kennis al voorhanden, en monitoringssystemen zijn reeds operationeel. De inspanningen hebben geleid tot een omvangrijke set gegevens over het voorkomen (soorten, biomassa en aantallen) van vele bodemorganismen en verschillende processen die zich in de bodem afspelen, op een aantal locaties met uiteenlopende grondsoort en bodemgebruik (Figuur 2). Ondanks dat de set met gegevens nog niet alle mogelijke variaties in bodemecosystemen bevat, kan er een begin worden gemaakt met de toepassing van bodembiologische inzichten voor de ontwikkeling van een raamwerk voor duurzaam bodemgebruik.

Op basis van metingen en berekeningen met BoBI op specifieke locaties kunnen kwaliteitsbeelden voor de bodem worden opgesteld. In situaties waar verondersteld wordt dat het bodemgebruik duurzaam is geweest, en waar volgens ecologische theorieën het ecosysteem stabiel is en een hoge bodemdiversiteit bevat, kunnen de BoBI metingen en berekeningen worden gebruikt om een referentiebeeld voor duurzaam bodemgebruik op te stellen.

In dit rapport is beschreven hoe een eerste set referentiebeelden voor het bodemecosysteem is afgeleid op basis van metingen en berekeningen met BoBI. Dit is gedaan voor één type bodemgebruik (melkveehouderij) en twee grondsoorten, namelijk grasland op zand en grasland op rivierklei. Op basis van het bodembeheer op de betreffende locaties èn op basis van ecologische theorieën kan aannemelijk worden gemaakt dat de bodemecosystemen volgens de berekende referentiebeelden duurzaam bodemgebruik indiceren. Dat betekent dat wanneer op een andere locatie met hetzelfde bodemgebruik en grondsoort een bodemecosysteem aangetroffen wordt met een vergelijkbare samenstelling, verondersteld mag worden dat het bodemgebruik op die locatie ook duurzaam is. Een bodemecosysteem met een vergelijkbare samenstelling kan dus als ‘gezond’ beschouwd worden. Uit de referentiebeelden voor duurzaam bodemgebruik kunnen streefbeelden afgeleid worden, waarbij de nutsfuncties in ruime of beperkte mate geborgd zijn.

De in dit rapport beschreven exercitie is de eerste in zijn soort, en de exacte betekenis van de referentiebeelden dient nog verder geëvalueerd te worden. Het is bekend dat variaties in het bodemecosysteem in tijd en ruimte groot zijn. Ook vormen van bodemgebruik en grondsoort kunnen sterk verschillen. De beschikbare set met bodembiologische gegevens is omvangrijk, maar toch nog te beperkt om al deze variaties te omvatten. Daarom zal in de nabije toekomst verder worden gewerkt aan de opbouw van het gegevensbestand met biologische, fysische en chemische bodemparameters op diverse locaties. Voor melkveehouderij op zandgrond (grootste areaal in Nederland) is de situatie relatief gunstig, omdat daar reeds veel gegevens over beschikbaar zijn. Daarnaast zal de gevolgde aanpak worden geëvalueerd op bruikbaarheid en integriteit, door de resultaten te toetsten in internationale wetenschappelijke gremia.



Figuur 2. Amoebe-diagram met diverse bodembiologische gegevens (Breure et al., 2003b).

Elke gekleurde taartpunt representeert een specifieke bodembiologische parameter. De grootte van de taartpunt geeft aan hoeveel de biologische parameter verschilt met die van een gekozen referentie (buitenste zwarte cirkel). Het binnenste zwarte gebied geeft aan waar een ernstig kwaliteitstekort dreigt.

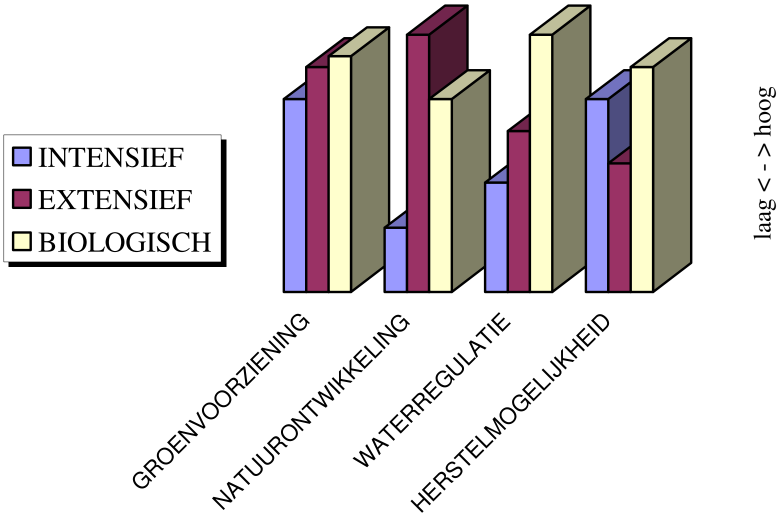
1.3 Afleiding van een kwaliteitstekort op basis van nutsfuncties

Uit de aanname dat een gekozen referentie een duurzame situatie indiceert (op basis van het relevante bodembeheer, bodembiologische gegevens en ecologische theorieën), volgt dat ook de nutsfuncties duurzaam zijn. Een afwijking van een referentiebeeld kan beschouwd worden als een gebrek aan bodemkwaliteit, of niet duurzaam bodemgebruik. Als de nutsfuncties gekwantificeerd worden volgens het schema in Figuur 1 met multicriteria analyse, is het mogelijk om per nutsfunctie het kwaliteitstekort in te schatten. Een bekend voorbeeld is het watervasthoudend en waterdoorlatend vermogen van de bodem. Door ploegen en berijden wordt deze nutsfunctie negatief beïnvloed, terwijl organische stof, regenwormen en bacteriën een positieve invloed hebben (Figuur 3).

1.4 Sturingsmaatregelen voor beheer en beleid

Met gegevens over de bodemkwaliteit in termen van nutsfuncties en duurzaam bodemgebruik kan de bodemkwaliteit meegenomen worden bij ruimtelijke planprocessen. Zo kan bijvoorbeeld onderscheid gemaakt worden tussen gebieden waar de bodem duurzaam gebruikt wordt (natuurgebieden en duurzame landbouw) en waar sommige nutsfuncties minder aandacht (behoeven) te krijgen (industrieterreinen). Daarnaast kunnen ambitieniveaus worden afgeleid, waarbij het gebruik van de bodem als ‘duurzaam’ beschouwd kan worden, zodat het niveau van de nutsfuncties op de langere termijn voldoende geborgd is. Met dit inzicht kan het bodembeheer (type bodembeheer, intensiteit van het bodemgebruik, en specifieke maatregelen) worden afgestemd op de ambities.

Voor het lokale bodembeheer kan inzicht in het kwaliteitstekort bij een nutsfunctie gebruikt worden voor specifieke sturingsmaatregelen op het niveau van een perceel of terrein. Dit aspect is tot op heden in het onderhavige project niet aan bod gekomen, maar zal in de nabije toekomst door het RIVM en andere partners worden uitgewerkt, bijvoorbeeld in een nieuw project ‘Bodem, Bedrijf en Biodiversiteit’.



Figuur 3. Kwaliteitsverschillen per nutsfunctie voor 3 vormen van bodemgebruik, namelijk grasland op zand bij drie veehouderijbedrijven Relatieve staafhoogte afgeleid met behulp van multicriteria analyse van bodembiologische parameters.

2. Uitgebreide samenvatting

2.1 Inleiding

In internationaal verband (EU, FAO, OECD, UNEP) is de aandacht voor de bodem toegenomen, door het besef dat het huidige bodemgebruik op alle ruimtelijke schaalniveaus onvoldoende duurzaam is. Momenteel wordt in EU verband gewerkt aan de *Strategic Soil Initiative*, maar het opstellen van een *European Soil Directive* is voorlopig uitgesteld. Desalniettemin wordt ook in EU verband het brede perspectief van duurzaam bodemgebruik als uitgangspunt voor het bodembeleid gehanteerd.

Zowel EU als VROM zijn voornemens om het beleid te richten op de duurzaamheid van het gebruik van de bodem en de ecologische processen in de bodem. Dit is een duidelijke beleidswijziging, want het ‘oude’ bodembeleid is gericht op de bescherming van de chemische bodemkwaliteit. In het oude bodembeleid zijn de kwaliteitscriteria gebaseerd op de concentraties en giftigheid van verontreinigende stoffen in de bodem. Ten behoeve van het nieuwe bodembeleid zullen de kwaliteitscriteria gebaseerd moeten zijn op de ecologische kwaliteit van de bodem. Ecologische kwaliteit is opgebouwd uit chemische, fysische en biologische aspecten. In het onderhavige project ‘Bodemecosystemen en kwaliteitsdoelstellingen’ wordt gewerkt aan de kwantificering van deze chemische, fysische en biologische parameters en aan de koppeling daarvan met ondergrondse biodiversiteit.

Ten behoeve van de uitvoering en toetsing van de effectiviteit van het bodembeleid is het gewenst om kwantitatieve criteria voor de bodemkwaliteit af te leiden. Dit is nodig om te kunnen beoordelen of de aanwezige kwaliteit voldoende is voor het gewenste gebruik, of voldoende is om op termijn het gewenste gebruik mogelijk te maken. Het gewenste schaalniveau (landelijk, regionaal of lokaal) is bepalend voor de mate van detail en specificiteit van de kwaliteitscriteria. De optimale of maximale kwaliteit van de bodem is verschillend, afhankelijk van de grondsoort en het bodemgebruik (zie ook Breure *et al.*, 2003a; 2003b; Mulder *et al.*, 2003a).

Dit rapport geeft een beschrijving van de methode voor de afleiding van de optimale samenstelling van het bodemleven in relatie tot grondsoort en bodemgebruik. Voor twee gevallen is dit specifiek uitgewerkt, en worden gegevens gepresenteerd. Hierbij is gebruik gemaakt van de monitoringgegevens die de afgelopen jaren verzameld zijn voor Bodembiologische Indicator (BoBI), alsmede inzichten over hoe een optimaal functionerend ecosysteem er uit zou moeten zien.

2.2 Koppeling van ecosysteemparameters aan het functioneren van de bodem

De wetenschappelijk kennis over het bodemecosysteem is de afgelopen jaren enorm toegenomen, dankzij doorbraken in de bodemecologie en bodemkunde, en de gerichte biologische meetinspanningen in het Landelijke Meetnet Bodemkwaliteit (LMB) en andere monitoringsactiviteiten. Recent zijn er vragen gesteld om een raamwerk te ontwikkelen voor duurzaam bodemgebruik naar aanleiding van de doelstellingen in het NMP4 en de aangekondigde wijzigingen bij het bodembeleid in de Beleidsbrief Bodem. Er is nog geen beleidsmatige overeenstemming hoe duurzaam bodemgebruik uitgewerkt moet worden. Op basis van bodembiologische gegevens (BoBI) en ecologische theorieën ontstaan momenteel wel mogelijkheden om op de gezondheid van de bodem en de duurzaamheid van het gebruik van de bodem vast te stellen. Van de Leemkule (2001) heeft de contouren van een raamwerk in een stappenplan uiteengezet.

Het begrip duurzaam bodemgebruik is niet van toepassing op natuurlijke systemen, omdat een systeem zonder menselijke beïnvloeding niet in termen van duurzaam gebruik gevat kan worden. Door de mens beïnvloede systemen zijn daarentegen niet waardevrij te beschrijven als het om duurzaamheid gaat. De volgende punten verdienen aandacht bij de ontwikkeling van een raamwerk.

1. De wetenschappelijke kennis over het functioneren van de bodem is omvangrijk, en ruim voldoende voor een grove indicatie van de bodemkwaliteit. Door het ontbreken van een voldoende robuuste, complete en integere ecosysteemtheorie, is de wetenschappelijk discussie over duurzaam bodemgebruik nog niet afgerond. Desalniettemin zijn er voldoende uitgewerkte ideeën om biodiversiteitsbeleid te ankeren in wetenschappelijke theorieën (vergelijk het wetenschappelijke debat over CO_2 en klimaatverandering).
2. De beschikbare kennis en hoeveelheid bruikbare gegevens is groot genoeg om indicatoren en referentiebeelden voor duurzaam bodemgebruik te ontwikkelen. Voor sommige combinaties van grondsoort en milieustress zijn nog weinig of geen (historische) gegevens voorhanden, en sommige nutsfuncties zijn lastiger te beoordelen dan andere. Er dient dus blijvend aandacht te worden besteed aan de opbouw van de kennisinfrastructuur als het om duurzaam bodemgebruik gaat.
3. Het maatschappelijke en beleidsmatige afwegingsproces om tot een kader voor duurzaam bodemgebruik te komen is nog niet afgerond. De inbreng van alle betrokken actoren bij beleid, beheer, gebruik en onderzoek van de bodem is van belang, omdat het afwegingsproces waardeoordelen in zich heeft.

Oplossing van de punten 1 en 2 vereist met name inspanningen die gericht zijn op kennisvermeerdering. Op verschillende fronten wordt hieraan gewerkt, door universiteiten en kennisinstituten, nationaal en internationaal. Deze inspanningen leiden er toe dat er steeds minder onzekerheden kleven aan het beoordelen van de duurzaamheid van het bodemgebruik. Bodemecosystemen zijn dermate complex dat alle informatie (chemisch, biologisch en fysisch) bijdraagt aan de beoordeling van de toestand (Lancaster, 2000). De oplossing is dus om alle beschikbare kennis pragmatisch toe te passen binnen het raamwerk voor duurzaam bodemgebruik, en niet slechts bodemchemische parameters te beschouwen.

Voor de oplossing van punt 3 zijn reeds de eerste stappen ondernomen, met name gericht op kennisoverdracht. Van de Leemkule (2001), de TCB (2000; 2003), Schouten *et al.* (2001) en Breure *et al.* (2003b) beschrijven de contouren van een raamwerk voor duurzaam bodemgebruik, gebaseerd op de ‘nutsfunties’ van het bodemecosysteem (Figuur 1). Van de Leemkule (2001) onderscheidt een aantal stappen om dit raamwerk volledig te ontwikkelen. Een van de stappen van het raamwerk betreft de koppelingen tussen het bodemgebruik, de nutsfuncties en de biologische, chemische en fysische bodemparameter, op basis van wetenschappelijke inzichten. Een belangrijk kenmerk van het raamwerk is dat het subjectieve elementen bevat, omdat waardering van ‘nutsfuncties’ op zich een subjectieve aangelegenheid is. Hoe nuttig is bijvoorbeeld een goede bodemstructuur voor het bodemgebruik en de maatschappij? En op welk niveau mogen we problemen verwachten? Deze vragen kunnen alleen beantwoord worden via een afwegingsproces waar beleidsmakers, bodemgebruikers, de maatschappij en deskundigen een rol in hebben. De laatste stap van het raamwerk (stap 10) betreft de werkelijke toepassing van het raamwerk, door beleidsdoelen vast te stellen of door het daadwerkelijk bepalen van de (on)duurzaamheid van het actuele bodemgebruik.

Voor de nadere uitwerking van het raamwerk is in eerste instantie een inventarisatie gemaakt van de nutsfuncties en de te onderscheiden typen bodemgebruik via een grove classificatie (Breure *et al.*, 2003b; Breure, 2004). In Tabel 1 is een schematische koppeling tussen het bodemgebruik en de nutsfuncties aangelegd. Er is nog discussie over de vraag of deze inventarisatie in voldoende mate de nutsfuncties van het bodemecosysteem dekt. Weinig genoemde ‘nutsfuncties’ zijn bijvoorbeeld het bodemecosysteem als specifieke basis voor natuur- en landschapsontwikkeling, esthetische functies, en lucht- en klimaatfuncties. Sommige nutsfuncties zijn minder belangrijk voor bepaalde typen bodemgebruik. Voor bijvoorbeeld een verharde bodem is de ziektewerendheid niet van belang. Het opleveren van een goede kwaliteit diep grondwater is voor het stedelijk gebied minder van belang. Overigens kan bij een nadere uitwerking blijken dat deze grove classificatie een meer specifieke uitwerking verlangt, conform de voorstellen van Rutgers *et al.* (1998) bij de (locatiespecifieke) beoordeling van bodemverontreiniging. Met de specifieke uitwerking per nutsfunctie is een aanvang gemaakt (zie ook: Breure *et al.*, 2003b en Markert *et al.*, 2003). In Tabel 1 staan de belangrijkste ‘nutsfuncties’ weergegeven, inclusief de koppeling naar bodembiologische aspecten, maar de uitwerking van de koppelingen dient nog plaats te vinden. Uit Tabel 1 blijkt dat veel (vergelijkbare) bodemecologische parameters betrokken zijn bij verschillende nutsfuncties, maar dit was te verwachten. Een gezonde regenwormengemeenschap is zowel van belang voor een goede bodemstructuurvorming (waterregulatie) als voor natuurontwikkeling met grote vogelpopulaties. Bij sommige nutsfuncties zijn volledig dezelfde ecologische parameters genoemd. Afhankelijk van de nutsfunctie zou de waarde van die parameter kunnen verschillen. Verder is het optimum afhankelijk van het bodemtype en van de gebruiksvorm.

Tabel 1: Overzicht van ecologische aspecten die indicatief zijn voor verschillende nutsfuncties (gedeeltelijk overgenomen van Breure et al., 2003b; Breure, 2004).

Nutsfunctie	**Belangrijke ecologische aspecten**
Levering voedingstoffen plant en dier	voedselweb incl. regenwormen primaire productie verhouding bacteriën/schimmels (de)nitrificatie
Waterregulatie (doorlaten èn vasthouden van water)	Regenwormen dichtheden en verhouding bacteriën/schimmels zuurgraad (pH); gehalte organische stof (SOM); grondwatertrap
Goede bodemstructuur	regenwormen, bacteriën/schimmels Channel Ratio van nematoden (Yeates, 2003) zuurgraad (pH), gehalte organische stof (SOM)
Levering schoon ondiep grondwater	specifieke activiteit bacteriën/schimmels schone bodem mate uitspoeling stikstof (N), fosfaat (P), gehalogeneerde verontreinigingen (EOX) stikstof (N)-cyclus
Levering schoon diep grondwater	hoeveelheid en biodiversiteit van bacteriën/schimmels mate uitspoeling stikstof (N), fosfaat (P), gehalogeneerde verontreinigingen (EOX) stikstof (N)-cyclus
Ziekte-werendheid in de landbouw	plant-parasitaire nematoden dichtheden en verhoudingen bacteriën/schimmels mycorrhyza-schimmels
Veranderbaarheid van het bodemgebruik	diversiteit van de bodemorganismen concentraties stikstof en fosfaat in de bodem
Stressgevoeligheid	biodiversiteit
In discussie: Onderlegger voor natuur- en landschapsontwikkeling	specifieke organismen (plant-insect interacties, bodemorganismen), vegetatie successie
In discussie: Luchtkwaliteit en klimaatfuncties (lokaal en regionaal)	strooiselkwaliteit, vegetatiestructuur, landschapsfragmentatie

Voor de koppeling tussen ‘nutsfuncties’ en de biologische, chemische en fysische bodemparameters is het nodig de nutsfuncties aan een nadere beschouwing te onderwerpen. Dit kan via het stappensysteem (Markert *et al.*, 2003). Op elk niveau, aangegeven met de diverse blokken, is een gerichte inspanning nodig om tot een bruikbare uitwerking te komen. Elke stap is nodig om met de objectieve inzichten en gegevens over het bodemecosysteem tot praktische en beleidsmatige toepassingen te komen in termen van indicatoren voor duurzaam bodemgebruik. Het onderscheid tussen vormen van bodemgebruik, nutsfuncties, regulatiefuncties, en de gecombineerde bodemgegevens (biologisch, chemisch en fysisch) is functioneel voor het raamwerk voor duurzaam bodemgebruik en biedt aanknopingspunten om binnen afzienbare tijd een eenduidig en toepasbaar systeem te ontwikkkelen.

2.3 Bodembiologische indicator

In de laatste decennia zijn veel inzichten ontwikkeld over de mechanismen die een rol spelen bij het verloop van de ecologische processen in de bodem. Veel van die functies worden (mede) ingevuld door de organismen in de bodem. Deze organismen leven samen in een ‘voedselweb’, waarbinnen ze functioneel aan elkaar gekoppeld zijn. Langzamerhand is er een behoorlijk inzicht in wie wat opeet (o.a. Cohen *et al*., 1993a; 1993b; De Ruiter *et al*., 1995; Mulder *et al*., 2005). Bij het ordenen van deze voedselrelaties ontstaan verschillende schema’s, waarvan een aantal is opgenomen in het Engelstalige deel van dit rapport. Voedselwebben worden gekenmerkt door het grote aantal interacties dat bestaat tussen (groepen van) organismen. Daarbij wordt ook zichtbaar dat sommige organismen gelijksoortige plaatsen in het voedselweb hebben. Zo zijn er verschillende soorten bacterie-etende nematoden, of plantenetende mijten, maar ook bijvoorbeeld plantenetende nematoden. Deze organismen worden dan op hun beurt weer door dezelfde of verschillende organismen gegeten. De ordening van al die organismen in een voedselweb kan op verschillende manieren:

A. via de beschrijving van de stromen van elementen door het systeem (bijvoorbeeld stikstof– en koolstofstroom), welk organisme zet hoeveel koolstof om, welk voedsel wordt er voor gebruikt, en wat is hun uitscheiding van stoffen.
B. via een allometrisch ordeningsprincipe van het ecosysteem: de ecologische niche, groei en nageslacht van organismen wordt niet alleen bepaald door hun voedsel, maar ook door hun specifieke dichtheid-gewicht relatie.

De beide benaderingen zijn schematisch weergegeven in het Engelstalige stuk. Een voorbeeld van de eerste benadering is het voedselweb zoals dat ontwikkeld is door Moore *et al.* (1988) en voor Nederland geadopteerd is door De Ruiter *et al.* (1995) wordt gepresenteerd in Figuur 7.

Om voor Nederland een beeld te krijgen van de samenstelling van het bodemecosysteem wordt door het RIVM in samenwerking met ALTERRA en de sectie Bodemkwaliteit van Wageningen Universiteit en Researchcentrum (WUR) gewerkt aan de ontwikkeling van de Bodembiologische Indicator (BoBI). Voor BoBI worden chemische, fysische en biologische gegevens verzameld (Figuur 2). De biologische parameters zijn geselecteerd op basis van de nutsfuncties van organismen in het voedselweb (Schouten *et al*., 2001). Deze gegevens omvatten:

- voorkomen van soorten (welke soorten komen voor en wanneer);
- dichtheden van soorten (hoeveel bodemorganismen van welke soort);
- activiteiten / processnelheden (CO_2 flux, potentiële C en N mineralisatie);
- bodemtype (zand, klei, veen) en abiotische omstandigheden (stressfactoren);
- type bodemgebruik (biologisch, extensief, intensief, akkerbouw etc.).

De metingen worden uitgevoerd in het kader van het Landelijk Meetnet Bodemkwaliteit (LMB) van TNO en RIVM. De locaties in dit meetnet zijn representatief voor ongeveer 70% van de combinaties van grondsoort en landgebruik in Nederland. Het overgrote deel van de 200 meetpunten in dit meetnet bestaat uit agrarische bedrijven (90%) en de bemonstering is op bedrijfsniveau. Op deze wijze worden jaarlijks 40-50 locaties geïnventariseerd en bodembiologisch gekarakteriseerd.

Bij de meting van de microbiële parameters zijn de potentiële C- en N-mineralisatiesnelheid bepaald. Dit zou kunnen worden gebruikt als een indicator voor de processnelheden. Omdat ook andere organismen hierbij en rol spelen, is dit nog maar een deel van de werkelijkheid. Gegeven de samenstelling van het bodemecosysteem kan met behulp van andere modellen een schatting worden gemaakt van de stikstof- en koolstofflux door het systeem. Echter, de databehoefte van dergelijke modellen is zo groot, dat wij daarvoor nog niet alle gegevens kunnen leveren en de modellen daardoor moeten aanpassen.

Op de volgende wijze is een direct verband te leggen tussen het voorkomen van organismen en de functie (bijvoorbeeld ‘structuurvorming’ in de bodem, of ‘levering van schoon grondwater’). Ons voorstel is om deze functies te kwantificeren als 100% in het ecosysteem met de optimale samenstelling, volgens de modellen van Cohen *et al.* (2003) en Mulder *et al.* (2005).

Er zijn vervolgens twee aanvullende methoden om te komen tot de kwantificering van de nutsfuncties in voorkomende gevallen met een daartoe speciaal ontworpen maatlat. De ene methode gaat uit van bestaande locaties en reële sets met bodembiologische gegevens. De andere methode gaat uit van de kennis en de visie van deskundigen op de uitvoering van nutsfuncties en de bijbehorende indicatoren (chemisch, fysisch en biologisch). Beide methoden zullen evenwichtig worden toegepast, zodat de beschikbare kennisvelden maximaal worden benut. Via een afwegingsproces waarin subjectieve elementen gebruikt worden, kan vervolgens de maatlat voor de nutsfuncties in bodemecologische eenheden (biologisch, chemisch en fysisch) uitgewerkt worden.

Vanuit de verschillende mathematische beschrijvingen van bodemvoedsel-webben kunnen criteria worden afgeleid voor de mate van stabiliteit van het systeem. In dit rapport is op basis van statistische verwerking van de monitoringsgegevens nagegaan, welke combinaties van organismen (i.r.t. hun massa en dichtheid) in verschillende bodemtypen stabiel zijn (Figuur 13), en in hoeverre we dergelijke systemen ook in het databestand kunnen terugvinden.

Met een landsdekkend beeld van referentiebeelden voor de bodembiologie, bodembiodiversiteit en bodemprocessen kan bodembeleid ontwikkeld worden. Uit de referentiebeelden kunnen streefbeelden worden afgeleid, waarbij de nutsfuncties in ruime of beperkte mate geborgd zijn. Op deze wijze kunnen de ruimtelijke aspecten van de bodemkwaliteit, in termen van de nutsfuncties, meegenomen worden bij ruimtelijke planprocessen. Zo kan bijvoorbeeld onderscheid gemaakt worden tussen gebieden waar de bodem duurzaam gebruikt wordt (natuurgebieden en eventueel landbouw) en waar sommige nutsfuncties minder aandacht (behoeven) te krijgen (industrieterreinen). Daarnaast kunnen in de toekomst ambitieniveaus worden afgeleid, waarbij de bodem duurzaam wordt gebruikt, als het huidige niveau van de nutsfuncties nu of op de langere termijn onvoldoende geborgd is.

2.4 Het gebruik van de referentiewaarden van de soortensamenstelling

Voor de afleiding van referentiesamenstelling van bodemleven is na evaluatie van verschillende ecologische theorieën uitgegaan van de aanpak van Cohen *et al.* (2003), waarbij de mate van stabiliteit berekend wordt aan de hand van voorkomen en dichtheid van organismen. Wanneer er meer predatoren zijn dan prooi is het systeem instabiel, omdat er niet genoeg voedsel is, andersom is het systeem inefficiënt omdat het aanwezige voedsel niet volledig kan worden gebruikt. Dit leidt vaak tot ongewenste ophoping van stoffen (bijvoorbeeld ophoping van organische stof in natuurgebieden door afwezigheid van soorten die dat kunnen afbreken). In een stabiel systeem is er een goede verhouding tussen prooi (voedsel) en predator.

Van 70 graslanden op zand zijn de monitoringsgegevens van ecosystemen doorgerekend om na te gaan in hoeverre zij voldeden aan de criteria voor stabiele ecosystemen. De biologische graslanden op zand bleken het meest aan die criteria te voldoen (Mulder *et al.*, 2003b, 2005). Daarnaast zijn de samenstellingen van 18 graslanden op rivierklei beschouwd. Van de beide groepen bedrijven is het bedrijf dat het meest voldoet aan de eisen van een stabiel ecosysteem gekozen als referentiesysteem. De twee referentiesystemen zijn in Tabel 2 samengevat.

REFERENTIE GRASLAND OP ZAND

	AANTAL	*TAXA*
Regenwormen (m^{-2})	$1.7\cdot10^{2}$	**3**
Potwormen (m^{-2})	$8.7\cdot10^{4}$	**4**
Nematoden (m^{-2})		**34**
Schimmel-eters	$1.6\cdot10^{5}$	
Bacterie-eters	$1.4\cdot10^{6}$	
Dauerlarven	$2.3\cdot10^{2}$	
Predatoren/omnivoren	$3.1\cdot10^{5}$	
Planten-eters	$1.8\cdot10^{6}$	
Microarthropoden (m^{-2})		**21**
Predatoren van arthropoden	$9.5\cdot10^{2}$	
Predatoren van nematoden	$1.7\cdot10^{3}$	
Algemene predatoren	$3.4\cdot10^{3}$	
Panphytophagen	$8.4\cdot10^{3}$	
Omnivoren	$2.2\cdot10^{3}$	
Bacterivoren	$9.5\cdot10^{1}$	
Bacteria (cellen kg^{-1})	$2.5\cdot10^{12}$	
Thymidine inbouw (pmol g^{-1} uur^{-1})	37	
Leucine inbouw (pmol g^{-1} uur^{-1})	512	
Pot. C-mineralisatie (mg kg^{-1} wk^{-1})	79	
Pot. N-mineralisatie (mg kg^{-1} wk^{-1})	9	
*Kolonietellingen (*CFU*) op agar*	$4.4\cdot10^{7}$	
Log CFU *50% kleuromzetting*	3.42	
ABIOTIEK		
*Pot. Aangetaste Fractie (*ms-*PAF)*	0.002	
P_2O_5–water (mg/l)	49	
*Zuurgraad (pH-*KCl*)*	5.3	
Organische stof (%)	8	
Lutum fractie (%)	1	
*GrootveeEenheden (*GVE *ha^{-1} jr^{-1})*	1.6	

REFERENTIE GRASLAND OP RIVIERKLEI

	AANTAL	*TAXA*
Regenwormen (m^{-2})	$1.3\cdot10^{2}$	**4**
Potwormen (m^{-2})	$3.1\cdot10^{4}$	**4**
Nematoden (m^{-2})		**28**
Schimmel-eters	$2.6\cdot10^{5}$	
Bacterie-eters	$1.0\cdot10^{6}$	
Dauerlarven	0	
Predatoren/omnivoren	$2.1\cdot10^{5}$	
Planten-eters	$2.0\cdot10^{6}$	
Microarthropoden (m^{-2})		**24**
Predatoren van arthropoden	$3.8\cdot10^{2}$	
Predatoren van nematoden	0	
Algemene predatoren	$1.9\cdot10^{3}$	
Panphytophagen	$1.0\cdot10^{4}$	
Omnivoren	$5.7\cdot10^{2}$	
Bacterivoren	$3.8\cdot10^{2}$	
Bacteria (cellen kg^{-1})	$6.4\cdot10^{12}$	
Thymidine inbouw (pmol g^{-1} uur^{-1})	65	
Leucine inbouw (pmol g^{-1} uur^{-1})	641	
Pot. C-mineralisatie (mg kg^{-1} wk^{-1})	136	
Pot. N-mineralisatie (mg kg^{-1} wk^{-1})	6	
*Kolonietellingen (*CFU*) op agar*	$5.8\cdot10^{7}$	
Log CFU *50% kleuromzetting*	1.99	
ABIOTIEK		
*Pot. Aangetaste Fractie (*ms-*PAF)*	0.010	
P_2O_5–water (mg/l)	27	
*Zuurgraad (pH-*KCl*)*	5.0	
Organische stof (%)	14	
Lutum fractie (%)	43	
*GrootveeEenheden (*GVE *ha^{-1} jr^{-1})*	1.4	

Tabel 2: Twee bodemecosystemen waarvan op basis van het relevante bodembeheer en ecosysteemtheorieën de veronderstelling is dat ze een gezonde bodem representeren voor grasland op zand en grasland op rivierklei.

De referentiesamenstellingen van de bodemecosystemen zijn bruikbaar als *benchmark*. Zij kunnen dienen om gewenste samenstellingen van het bodemecosysteem af te leiden. Op basis van de monitoringgegevens kan voor ieder organisme, dat op voldoende plaatsen is aangetroffen, via Gegeneraliseerde Lineaire Modellen (GLM) een habitat-respons-relatie worden afgeleid (Mulder en De Zwart, 2003). Daarmee kan ook worden aangegeven welke beheersingrepen nodig zouden zijn om van de huidige naar de gewenste situatie te komen. De mate van de stabiliteit van het systeem kan worden bepaald door de monitoringsgegevens in te voeren in het gebruikte model en te vergelijken met het referentiesysteem.

De gepresenteerde referenties voor bodemecosystemen in Tabel 2 geven een relatief compleet beeld voor wat betreft de biologische samenstelling van het bodemecosysteem. Het is van belang te onderkennen dat naast de biologische ook chemische en fysische hoedanigheid van de bodem van belang is voor duurzaam gebruik van de ecologische diensten van de bodem. Deze zijn bij deze exercitie vooralsnog buiten beschouwing gebleven. Tevens dient opgemerkt te worden dat het niet per sé noodzakelijk is om altijd alle biologische parameters af te leiden, en dat met een beperkt set (biologische) parameters ook tot een kwaliteitsoordeel gekomen kan worden. Met een dergelijke beperkte inzet komt de lokale toepassing van een raamwerk voor duurzaam bodemgebruik in beeld.

2.5 Discussie en conclusie

Op basis van ecologische inzichten en de monitoringsgegevens die verkregen zijn in het kader van de ontwikkeling van BoBI is het mogelijk referentiebeelden voor bodemecosystemen te beschrijven. Voor graslanden op zand en graslanden op rivierklei is dat in dit rapport uitgewerkt, op basis van de bodembiologische gegevens van het Landelijk Meetnet Bodemkwaliteit (LMB), en geaccepteerde ecologische theorieën. Onder de paraplu van het Platform ecologische risicobeoordeling (PERISCOOP, 2003) zijn ook referentieecosystemen ontwikkeld voor de beoordeling van bodemverontreiniging, namelijk één voor een grasland in Uiterwaarden en één voor een aquatisch bodemecosysteem met ondiep slib.

Het verloop van de ecologische processen of nutsfuncties kan worden aangegeven op een relatieve schaal, waarbij het doelecosysteem op 100% wordt gesteld. In het vervolg van deze studie zal het databestand moeten worden uitgebreid om referentiebeelden in meer combinaties van grondsoort en bodemgebruik te kunnen afleiden. Wanneer duidelijk is wat de verschillen en overeenkomsten zijn van de soortensamenstellingen in ecosystemen, kan ook worden bepaald of het op termijn noodzakelijk en mogelijk is om het meetprogramma voor de vaststelling van de ecologische kwaliteit aan te passen en zo mogelijk te vereenvoudigen. Verder moet aan modelontwikkeling worden gedaan, om op basis van de soortensamenstelling de flux van nutriënten door het systeem te schatten.

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3. Historical background

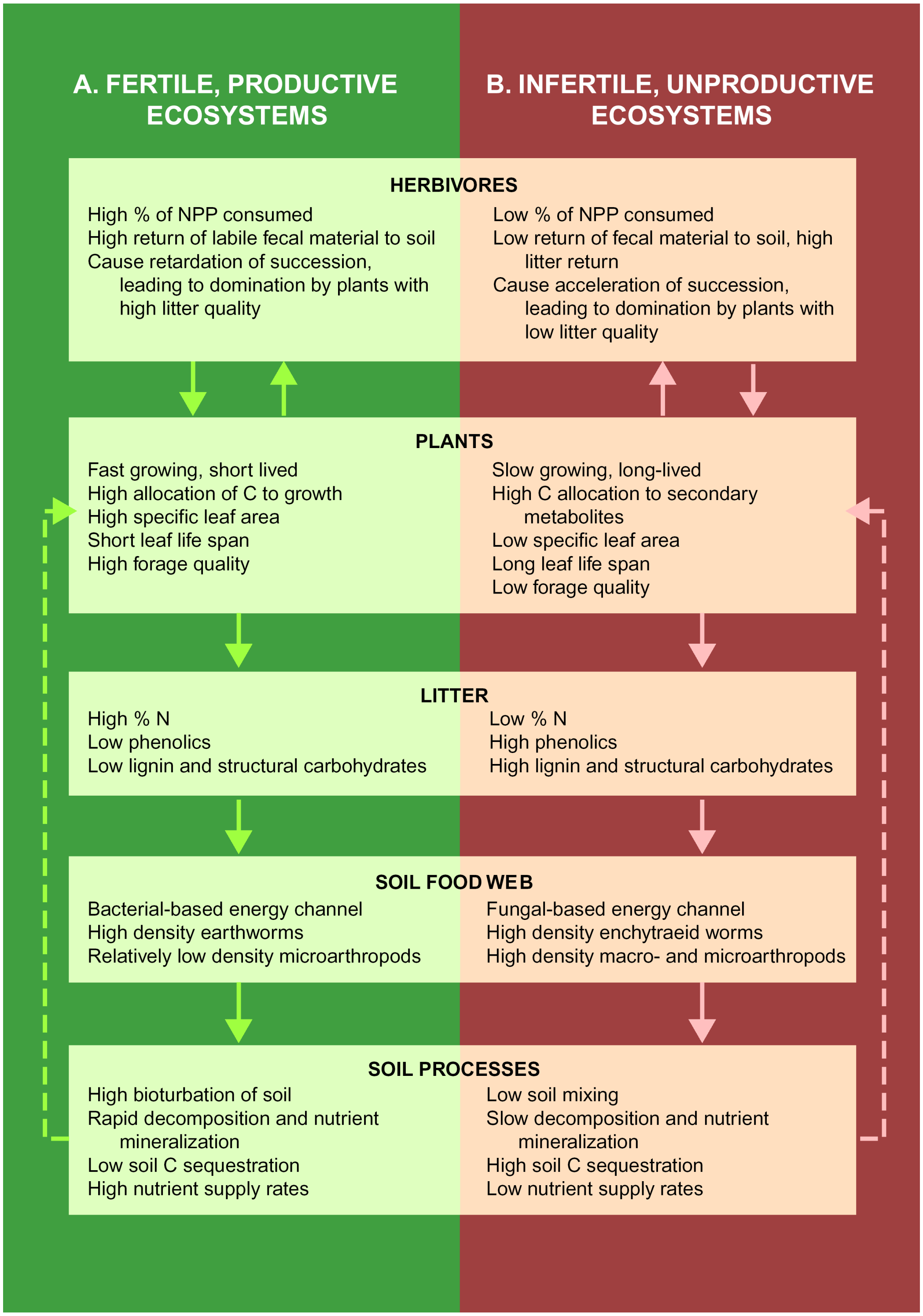
Soil organisms provide objective metrics for biological soil quality that integrates physical and chemical variables with biogeography and macroecology. The specific goal of soil policy is the sustainable use of soil. That comprises the conservation of biodiversity in the soil and the assurance of Life Support Functions of the soil (Schouten *et al*., 2001). Both are the basis for sustainable land use. To be able to conduct soil policy it is necessary to have a technique to quantify ‘the quality of soil’ and the sustainability of soil use. Soil quality is composed of a combination of factors. It cannot be indicated by single species or single taxa but can be defined by quantification of the deviation from a reference state. The definition of reference states comprises three steps: the ecological classification of sites, the recognition of bioindicators among the observed species and their subsequent assignment to predicted abundances and processes.

Despite mutual benefits, these three steps evolved separately, as most field ecologists focused rather on the biological classification of sites in communities, most ecotoxicologists paid attention to the identification of effective and cheap proxies, and most theoretical biologists developed mathematical models for (sometimes arbitrary) parameters. As a direct consequence, the correlation and extrapolation of these three steps may appear difficult, although the histories of ecological classification and applied ecology are closely linked since the 19th century. Already De Candolle (1855) recognized a key-role of winter temperature in the distribution of oceanic vascular plants. Such correlation-features established, beyond reasonable doubt, that climate is a determinant factor for the distribution of species. A second question to be answered occurred soon: to what extent can other correlation-features become determinant at large scales? There is increasing evidence of serious problems in the world’s agricultural areas. Historical attempts to increase agricultural production caused on one hand a debate among scientists started by Von Liebig in 1840 (!), on the other hand a kind of pragmatism in agriculture and forestry. This bifurcation originated other problems. Nowadays, Pimentel *et al.* (1987) and Kendall and Pimentel (1994) see already one third of Earth’s surface as degraded and the soil erosion is worsening by high-pressure agriculture and excessive forest management. Biodiversity loss is another actual problem, as we do not know how fast we are approaching strong shifts. Ecological modelling is in fact highly ineffective for the conservation of individual species (Botkin, 1990), as singular species do never thrive apart from other species occurring in their ecosystem. If these different species enable the system to persist in nominal behavioral states as long as or longer than its expected natural longevity (Costanza *et al.*, 1997: p. 98), we may describe the features (species, functional processes and ecological services) as related to sustainable development.

As most ecological studies advocate that the distribution, abundance, and dominance of a given taxon under certain environmental conditions reflect both the response of the local population to environmental stress and the extent to which local habitats meet primary niche requirements of a taxon, it becomes possible to summarize any variation in the community structure and in taxonomic richness by grouping together similar areas. However, several problems may occur during functional studies at different trophic levels. For instance, the mobility of animals remains an intrinsic problem in the delimitation and the classification of communities. In the case of detritivore organisms, however, this problem is limited. Actually, this means that the physical structure of the soil (porosity, clay fraction, bulk density) plays an important role in the comparison between studies, sites, microflora and bacterivore organisms. Besides this applied aspect of spatial food-webs, we will subsequently discuss the implications that follow when linear regressions that span a wide body size range are applied to the observed abundance of soil organisms. Starting point was always the observation that soil animals are not randomly distributed but that their body mass (*M*) and numerical abundance (*N*) are correlated with environmental properties (Ghilarov, 1944, 1965) and are not independent (Cohen *et al.*, 1993a, 2003). The allometric scaling for population density and organism size provides not only initial values for specific food-web models, but also a unique possibility to define reference sites. Thus, concrete systems representative in their abiotic and biotic properties as well as their faunal composition for a range of real sites are defined as ‘the condition that is representative of a group of minimally disturbed sites defined by selected physical, chemical and biological attributes’ (Reynoldson *et al.,* 1997).

Soil organisms, in particular non-parasitic nematodes, have been thoroughly investigated during the last 20 years. Enrichment and structure indicators for environmental health and ecological amplitude showed a great evolution. Faunal indices, ranging from a continuous ranking according to the estimated dominant life strategy of nematodes (Bongers, 1990, 1999) up to the trophic-based Nematode Channels as originally defined by Moore and Hunt (1988), Yeates (2003) and Yeates *et al.* (2003), can be chosen to assess possible disturbance effects on the basal fauna and to express the energy efficiency in soil decomposition processes (Yeates and Bongers, 1999). Links and driving processes between above-ground vegetation and below-ground organisms have been recognized and carefully described (extensive reviews in Wolters *et al.*, 2000 and Wardle, 2002). However, as the (cascade) effects vary strongly and clear evidence of *constant* top-down and/or bottom-up regulation is still lacking, a dichotomy has to be made with a group of character states or functional traits on one side (fertile, productive systems) and an opposite group of states/traits on the other (in our case, unproductive systems). Ideally, Wardle *et al.* (2004) depicted these traits and links to Net Primary Production (NPP) in a convincing way (Table 3).

Table 3. Plant traits serve as determinants of the quality and quantity of litter and the subsequent key ecological processes occurring in the soil.



	A. FERTILE, PRODUCTIVE ECOSYSTEMS	B. INFERTILE, UNPRODUCTIVE ECOSYSTEMS
HERBIVORES	High % of NPP consumed High return of labile fecal material to soil Cause retardation of succession, leading to domination by plants with high litter quality	Low % of NPP consumed Low return of fecal material to soil, high litter return Cause acceleration of succession, leading to domination by plants with low litter quality
PLANTS	Fast growing, short lived High allocation of C to growth High specific leaf area Short leaf life span High forage quality	Slow growing, long-lived High C allocation to secondary metabolites Low specific leaf area Long leaf life span Low forage quality
LITTER	High % N Low phenolics Low lignin and structural carbohydrates	Low % N High phenolics High lignin and structural carbohydrates
SOIL FOOD WEB	Bacterial-based energy channel High density earthworms Relatively low density microarthropods	Fungal-based energy channel High density enchytraeid worms High density macro- and microarthropods
SOIL PROCESSES	High bioturbation of soil Rapid decomposition and nutrient mineralization Low soil C sequestration High nutrient supply rates	Low soil mixing Slow decomposition and nutrient mineralization High soil C sequestration Low nutrient supply rates

Linkages between below- and above-ground systems feed back (dotted line) to the vegetation positively in fertile conditions (green) and negatively in unproductive ecosystems (brown). Reproduced from Wardle *et al.* (2004) with gently permission.

In practice, the dichotomy of Table 3 never occurs so strictly. If it did, environmental assessment would be greatly facilitated and use of sophisticated numerical methods hardly necessary. Although debated, the transformation of species-poor (productive) grasslands in (less-productive) species-rich grassland remains a current practice above-ground in conservation ecology and restoration management (Bakker, 1989; Brussaard *et al*., 1996; but see Swift *et al*., 1996). From a pragmatic point of view, this dichotomical concept could be used in multicriteria analysis. However, if so, we have to take into careful account that some key Life Support Functions are rather unpredictable in the soil. For instance, Wardle *et al*. (2004) couple a relative fungal dominance in the soils to N-poor litter, whereas often the opposite occurs, at least for fungal diversity and spore production (Mulder *et al*., 2003a; but also see Jansa *et al.*, 2002 and Wardle, 1995 for soil tillage). On the other hand, bottom-up effects are widely described in literature and are supported by laboratory evidence for extremely effective competition between microbes and plants for the N-uptake (e.g., Setälä *et al.*, 1998; Laakso *et al.*, 2000). Actually, the difference between 'slow' and 'passive' pools in the soil is striking. As only some bacteria are –like plants– photoautotrophic organisms, most of the microorganisms are heterotrophic (Figure 4). Thus, when plant litter reaches the soil (surface litter) or is detached/consumed from the rhizosphere (root litter), the heterotrophic respiration starts with the decomposing process of converting the organic carbon in the litter to CO_2 (Figure 5), making nitrogen available for plants. The decomposition rate is influenced by the chemical nature of carbon (cellulose *vs*. lignine) and by the microbial pools (Figure 6). These key cycles support the life of all organisms (Beerling and Woodward, 2001; Moore *et al*., 2004). A further stabilizing effect of detritus can be achieved not only through self-limitation of the resource (as in primary-producer models) but rather as the result of a constant input (Neutel *et al*., 1995; Moore *et al*., 2004). Yet, empirical evidence is lacking. Thus, all these driving processes (and coupled ecosystem services) necessitate a field-investigation. We have chosen as starting point for the development of indicators:

- degradation of organic material (generate soils and renew their fertility),
- recycling and availability of nutrients (cycle and move nutrients),
- soil structure evolution (bioturbation and aggregate formation, water retention),
- stability of the below-ground ecosystem (maintain biodiversity, control pests).

From a scientific point of view, the life support concept can be an operational approach for the protection and sustainable use of soil biodiversity (Breure *et al.*, 2003a, 2004). Policy goals can be formulated on the basis of deviation from a chosen reference situation. Realization of the indicator system depends on the need of information, the available finances, and the control through research programmes by the ministries involved. The indicative variables are potential rates of several processes, and biodiversity within and abundance of functional groups. We based the indicator system for Life Support Functions in the soil on the following hypothesis: *The threat to vital soil processes can be expressed by comparing the number of species in functional groups in a certain area with its reference* (Breure, 2004).

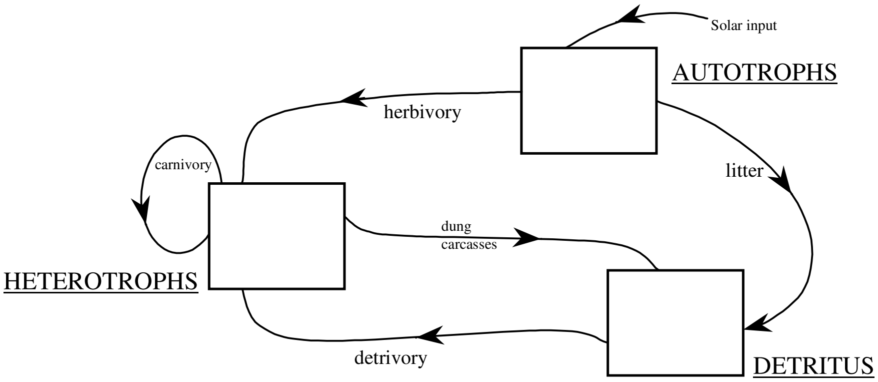


Figure 4. The three fundamental categories of the trophic continuum according to Cousins (1985, mod.): phototrophs (producers: almost all plants and autotrophic bacteria), chemo-organotrophs (consumers and predators: animals, and saprophytic bacteria and fungi), and dead (organic) detritus.

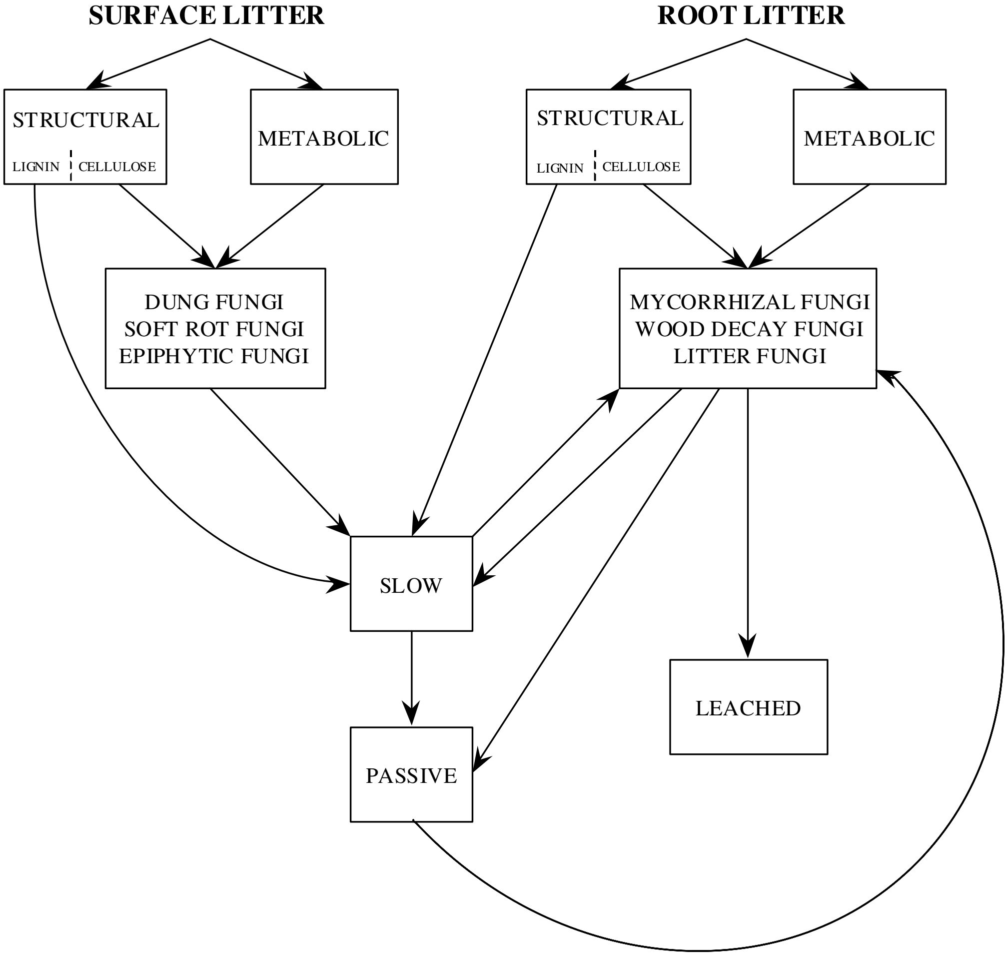
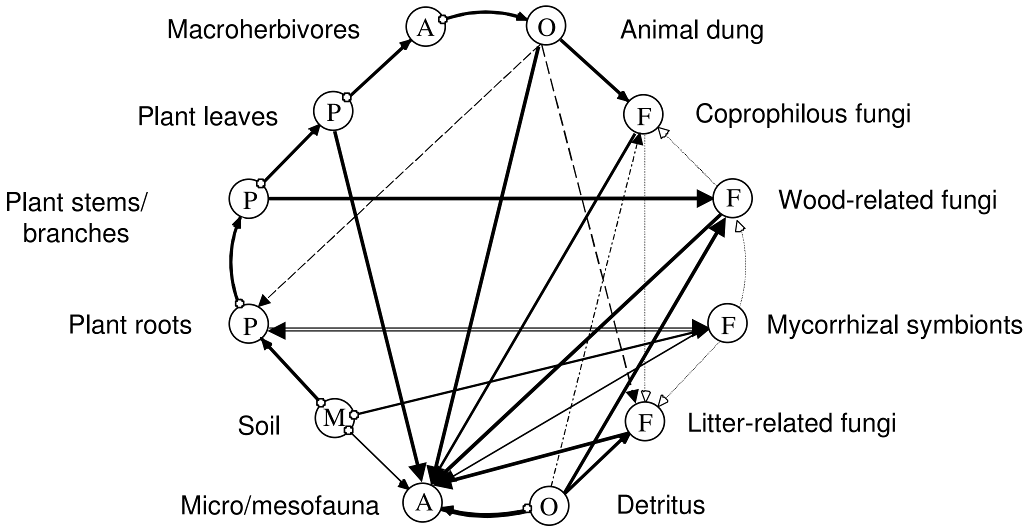


Figure 5. Structure and carbon-pathways in the litter/detritus interface (improved from Beerling and Woodward, 2001). Passive detrital channel soil in the center of the figure vs leached C on the right.

A) Trophic chains and energy flow



B) Chemical interactions and feedbacks

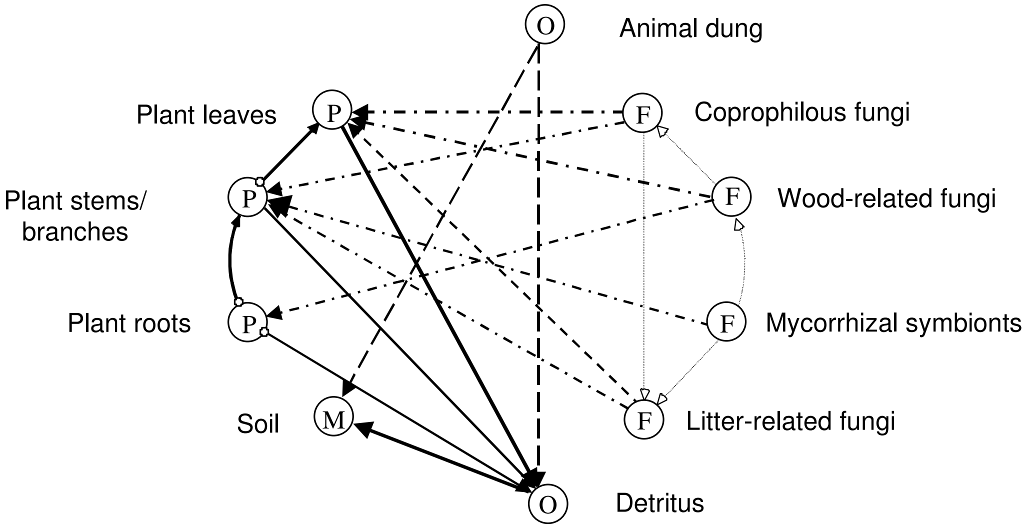


Figure 6. Energy flow and feedbacks (Mulder and De Zwart, 2003).

The arrows point out the direction and the importance of a given interaction (airborne dispersal of fungi as dashed lines). Dominant and secondary trophic habits of 30 palynologically identified soil fungi as defined in Mulder *et al*. (2003a). Counterclockwise, O = Organic substrates (dung or detritus), F = Fungal communities, A = Animal communities (Above-ground: Macroherbivores; Below-ground: Soil decomposers), P = Plant components, M = Mineral substrate (compare with Figure 5).

4. Ecological modelling

Stress is supposed to have little effect on the soil system due to a widespread stabilizing feedback. Scheffer *et al.* (2001) described alternative stable states (representing the state of the ecosystem) as a ball that tends to settle between tops corresponding to unstable equilibria. This up-and-down movement of the ball represents condition changes that affect the landscape and its stability. The restoration of the original environmental conditions before changes occurred is not *per se* sufficient to induce a shift back (hysteresis) of the ecosystem. Therefore, even constant environmental conditions can not be seen as really stable states, as their stability is not a static condition, but a dynamic process, even if the trends are slow. Carpenter (2002) suggests therefore to avoid the term equilibrium, as this word seems to exclude any form of dynamics. The resulting stability is not only due to the effects of stress on organisms, but can also be ascribed to the phenology of organisms, i.e., seasonality, weather fluctuations, and sampling period. Any system reacts at the same time to continue changes (long-term trends) as to abrupt perturbations (short-term trends). This reacting capacity to incorporate these environmental changes is the resilience of an ecosystem (or community). Like sustainability, also a high resilience is regarded as desiderable. However, resilience differs from sustainability, as both desirable and undesirable system states can be resilient.

Sustainable development remains the overarching goal based on assumptions about which system state is desirable (Carpenter *et al.*, 2001; Walker *et al.*, 2002) and depends on the temporal trends and spatial patterns of the investigation. Therefore, both the sensitivity of a food-web to changes as the efficiency of a food-web under environmental pressure have been investigated carefully. About one decade ago, De Ruiter *et al.* (1993ab, 1994) introduced the detrital soil food-web of Hunt *et al.* (1987) in the Netherlands. In many Dutch environments, the results of these models at the level of overall respiration and mineralization fluxes are extremely reliable. Still, in a recent review of Dekker *et al.* (2005), attention is given to the somewhat overwhelming weight of the fluxes that occur within microorganisms (bacteria, fungi and protozoans), as most other below-ground consumers and predators (nematodes, micro-arthropods etc.) have an insignificant direct effect on the fluxes computed by this model. An intriguing new point is that other ways have to be explored to state the extent to what ecosystems can be regarded as ‘stable’ (*sensu* Moore and Hunt, 1988).

Besides the necessary elements for the interaction matrix (and the inverse matrix) of a given community, Berlow *et al.* (2004) stated in their review that both theoretical and empirical investigations have to include:

(1) elements of the community;
(2) biomass flux;

(3) relative prey preference;
(4) consumption rate and frequency;
(5) link density;
(6) correlations among numerical abundances of populations, and
(7) effects on numerical abundances from perturbation to secondary extinction.

Actually, although we are still missing field and microcosm information to fulfill the elements 3 and 4 (relative prey preference, maximum consumption rate and consumption frequency), we can follow two parallel roads: (A) continue to focus on the elements 1 and 2 using De Ruiter's detrital food-web model (Figure 7), and (B) make an attempt to unravel the elements 5, 6 and 7 using Cohen's model (Figure 8). To a certain extent, both figures rely on the two main energy channels of Table 3, the bacterial energy channel (where the soil nematodes and litter protozoans have the greatest potential to affect it) and the fungal energy channel (where the micro-arthropods have the greatest potential to affect it).

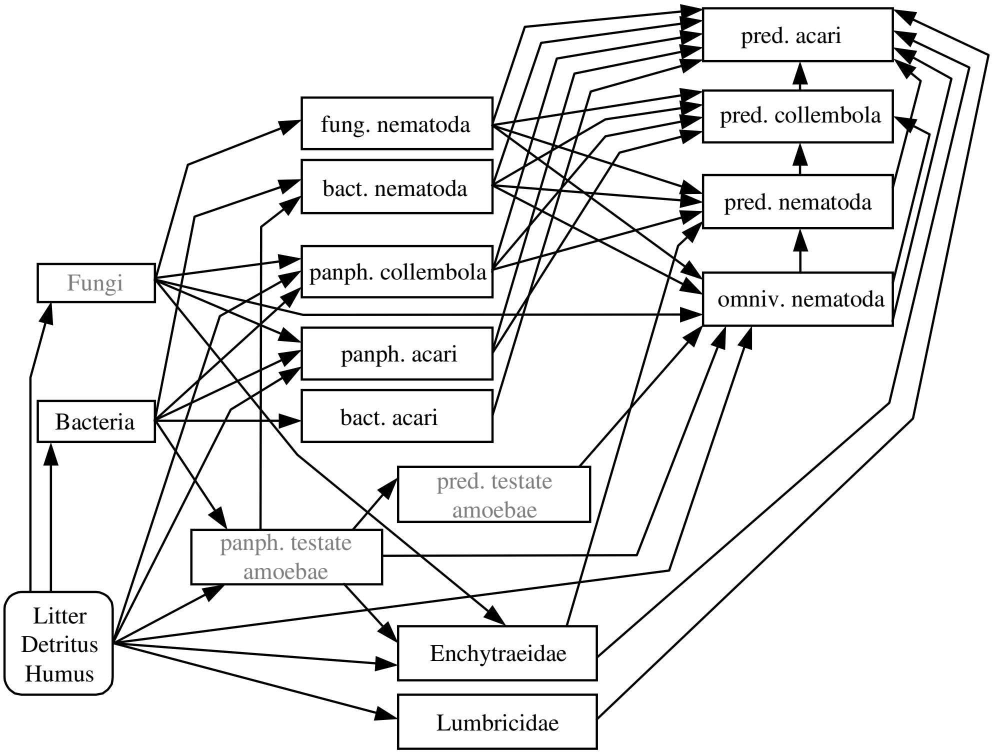


Figure 7. Typical connectedness web of the detrital soil food-web in a Dutch organic grassland on sand sampled in 1999.

Sketch of the food-web modified from De Ruiter *et al.* (1995) and Schröter *et al.* (2003). Fung. = Hyphal-feeding; bact. = bacterial-feeding; panph. = panphytophagous (feeding on microflora and plant debris); omniv. = omnivorous; pred. = predaceous. Main feeding relationships according to Moore *et al.* (1988), Yeates *et al.* (1993), Schönholzer *et al.* (1999), Bonkowski (2004), and microcosm manipulation from Mulder and Setälä (unpublished data). In the framework of the Dutch Soil Quality Network (DSQN), fungi and amoebae (grey) are not measured.

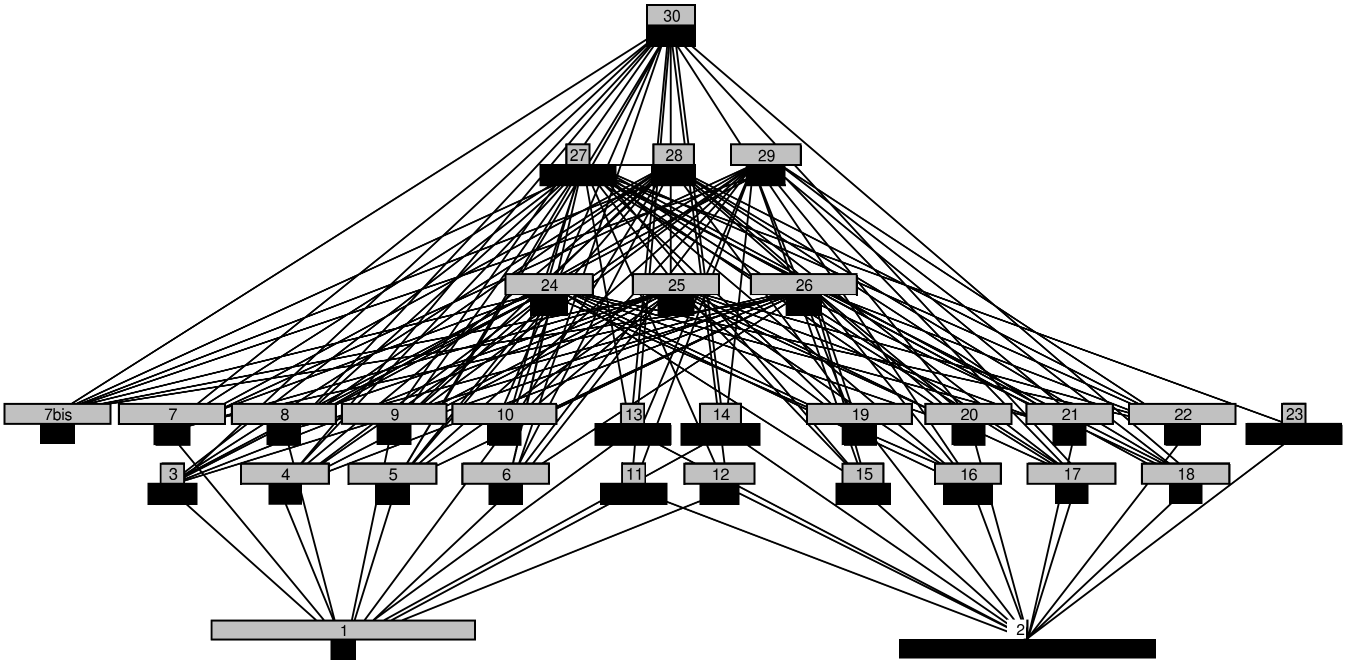


Figure 8. Example of different parameters for a food-web description in a terrestrial environment under low management pressure, in our case numerical abundance, body mass and links of soil organisms occurring in 1999.

The width of the black and grey horizontal bars shows for each taxon the relative rank of the $\log_{10}$ body mass M (kg) and the $\log_{10}$ numerical abundance N (individuals per kg soil), respectively. The larger the black (grey) bar, the greater (abundant) the organism. The left of the previous figure is depicted here at the bottom of the food-web, namely the resources (1 = bacteria and 2 = detritus). At the top of the food-web the predators –mostly micro-arthropods– are shown; those intermediate are omnivores (nematodes). Numbers in grey bars refer to taxa: 3 = *Histiostoma*, 4 = *Diplogasteroides*, 5 = Panagrolaimidae, 6 = *Alaimus*, 7 = Rhabditidae (Dauerlarvae as 7bis), 8 = Teratocephalidae, 9 = Plectidae, 10 = Cephalobidae, 11 = *Isotoma*, 12 = *Eupelops*, 13 = *Hypogastrura*, 14 = *Sminthurinus*, 15 = *Henlea*, 16 = *Enchytraeus*, 17 = Anguinidae, 18 = Aphelenchoididae, 19 = Dolichodoridae, 20 = *Paratylenchus*, 21 = Trichodoridae, 22 = Tylenchidae, 23 = *Lumbricus*; 24 = Qudsianematidae, 25 = *Tripyla*, 26 = *Dorylaimus*, 27 = Uropoda, 28 = *Alliphis*, 29 = *Arctoseius*, 30 = Scutacaridae. Both this plate as the previous one (Figure 7) show –in a different way– all data available for organisms occurring in the same bio-farm. Aside the resources (bacteria and detritus), this pyramidal structure resembles closely aquatic networks (e.g., Winemiller, 1990; Cohen and Carpenter, 2005).

A further elegant way to describe the energy flux that occurs below-ground is the use of a third energy channel (plant roots) to describe the energy flux (Figure 9). However, the latter procedure –as originally proposed by Hunt *et al.* (1987)– demands much information about the individual ecophysiology of each component. As evidence of important consequences for the stability of a food-web of the actual distribution of body mass across trophic levels is increasing, we have chosen for the second procedure, as it allows the recognition of altered magnitude of interaction strengths in the propagation of stress effects and disturbances.

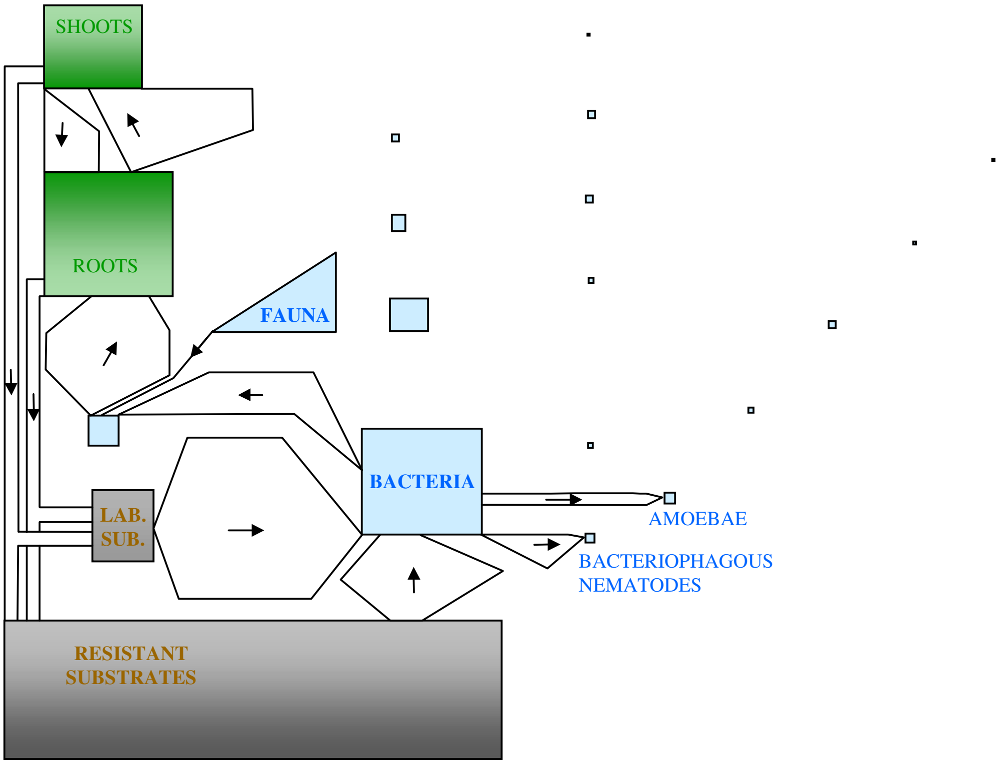


Figure 9. The energy flux description of the detrital soil food-web of a native shortgrass steppe in NE Colorado (Hunt et al., 1987).

Vectors and compartiments are sized according to the nitrogen flow (g N m^{-2} $year^{-1}$) and functional biomass (g N m^{-2}). Although this prairie is faunal poor, the faunal biomass turnover is very high. Note the three distinct energy channels, plants (roots, affects mainly plant-feeding nematodes), fungi (affects hyphal-feeding nematodes and all micro-arthropods, inclusive predator mites), and bacteria (bacteriophagous, omnivore and predator nematodes, nematophagous and predaceous mites, flagellates, ciliates, testate amoebae). However, the proportion of energy potentially derived in nutrient-rich agroecosystems like in the Netherlands is highly different from those derived in most American steppes, at least due to the huge differences in labile substrates (LAB. SUB.) and a higher soil biodiversity (i.e., higher functional redundancy among decomposers).

Box 1. Stable states do not exist, either in agroenvironments or in nature. Even under environmental conditions that are hold constant for a certain time span, the ecosystem functioning and the ecosystem stability are part of a continuous, dynamic process. Although unobtainable, policy-makers aim ‘static conditions’. The assessment of the efficiency in process regulation in the detrital soil food-webs enables to provide an answer to this management question. Paine (1980) categorized food-web modelling as connectedness webs, energy-flow webs or functional webs. We have chosen for a study that is supposed to show whether community differences in the density-body mass relationships are large enough to influence the ecosystem functioning and the ecological services of the soil biota.

5. Material and Methods

5.1 Soil sampling/data collection

Soil organisms are sampled within the Dutch Soil Quality Network (DSQN). The main aim of DSQN is to obtain information regarding soil status and trends. It covers a site selection representative for 70% of the surface area of the Netherlands (regarding soil type and land use). A complete field sampling 'round' takes five successive years. This network was originally designed to collect data on soil's abiotics (soil moisture, acidification, nitrification etc.), and it contains 240 locations with 12 soil type / land use combinations (20 replications) and 50 additional sites. Every year 40 locations are sampled. The major part of the sites is rural, comprising the following combinations of soil type and land use:

Pasture land on sandy soil (diary cattle farms):

1. *Grasslands under organic management* (in Dutch: 'biologisch')
2. *Grasslands under conventional management* ('extensief')
3. *Grasslands under semi-intensive farming regime* ('intensief')
4. *Grasslands under very intensive farming regime* ('intensief +')

Others:

5. Pasture land on peat soil
6. Pasture land on river clay
7. Pasture land on marine clay
8. Arable farming on sand
9. Arable farming on clay
10. Horticulture
11. Forests (pine plantations)
12. Nature (heaths, grasslands).

Within this network, the following taxonomic groups and functions have up to now been assessed in the laboratories of the RIVM and ALTERRA:

1) microorganisms: number, biomass, activity, genetic diversity, functional diversity (BIOLOG^{TM}) and potential C and N mineralisation rate;
2) nematodes: number, biomass, diversity, feeding habit;
3) enchytraeids and earthworms: number, biomass, diversity;
4) mites and springtails: number and diversity, functional guilds.

All these data has been linked to local measurements of: pH, organic matter, lutum (clay particles < 2 µm), soil humidity, plant available phosphorous, and heavy metals (Cd, Cr, Cu, Hg, Ni, Pb, and Zn), and ranked according to the land-use of the investigated farms. Data on biodiversity and numerical abundance of soil organisms, together with abiotic conditions and management data of the sampling sites, provide a unique facility to accurately determine the key processes and linkages between them, as well as the species interactions and their sensitivity to abiotic gradients. Such datasets are essential for high-resolution records of soil micro- and mesofauna that can be uninterruptedly linked to land-use in order to estimate the actual impact of farming pressure on soil biodiversity. Our main goals are to identify and evaluate:

(a) key environmental processes on soil biodiversity and ecosystem functioning,
(b) taxa and habitats that are most vulnerable to the loss of soil biodiversity, and
(c) soil habitats that are most amenable to effective restoration.

5.2 Collection and weighting of the soil organisms

Spatial patterns of both the active microbial biomass and the consumers provide a fine-tuned assessment of the basal soil quality in the Netherlands. To achieve this, bacteria, nematodes, mites, collembolans, enchytraeids, and earthworms were collected across the investigated agroecosystems between 1999 and 2003. Our basic sampling units were 110 managed grassland farms on Pleistocene sand and 40 on river clay. On each farm, 320 soil cores were taken randomly and mixed in a plastic container. Nematodes were extracted from 100 g soil using funnel elutriation, sieving and cottonwool extraction (Schouten *et al.*, 2004). Two clean suspensions in 10 ml water were screened with a stereomicroscope to count all individuals. In two permanent mounts in formaldehyde, 150 individuals were counted in total. Soil nematodes were identified at genus level by light microscopy (400-600x) and subsequently assigned to feeding guilds according to Yeates *et al.* (1993). Nematodes (bacterivores, herbivores, fungivores, predators/omnivores) have a numerical abundance of 10-50 individuals g^{-1} and a biomass up to 1 kg C ha^{-1}.

Micro-arthropods were also collected in a randomized block design and their four-fold cores (diameter 5.8 cm x 5 cm) were kept separate until behavioral extraction. The animals were subsequently sampled, observed at a magnification of 200-1,000x with a light microscope and assigned to feeding guilds on the basis of their carbohydrase activity (Siepel, 1994; Siepel and De Ruiter-Dijkman, 1993; Siepel and Maaskamp, 1994). Mites (bacterivores, panphytophagous, omnivores, and predators) have a numerical abundance of about 10^4 m^{-2} and a biomass up to 0.1 kg C ha^{-1}. Collembolans (fungivores, omnivores) have a similar numerical abundance as mites, but the total carbon content of their body mass differs one order of magnitude from those of mites, raising up to 1 kg C ha^{-1}. It should be emphasized that a high amount of our knowledge about diet range has been derived from microcosm studies using few selected organisms. Micro-arthropods were extracted with Tullgren funnels and divided in body size classes. The corresponding dry weight per body size class was calculated based on regression equations of length on dry weight (Berg *et al.*, 2001). Earthworms consume detritus only, being their ingestion of bacteria passively related to their feeding on soil particles. Enchytraeids are relatives of earthworms with a much smaller size and the same diet. Their densities are comparable with those of the mites, with a carbon content similar to those of the collembolans. Enchytraeids were extracted using wet funnel extraction, whereupon animals were identified, measured and counted. In all cases, the averages of our body mass values (we have chosen not to use the mean adult body size) have been computed at genus level as this taxonomical resolution offers the highest environmental information and the lowest structural noise (Figure 10). Obviously, the biomass B of a genus is its body mass M times its numerical abundance N. All our values of body mass M have been desumed from the average of the dry weight of litterbag grown specimens, including juveniles and resting stages, although in the case of some rarely occurring nematode taxa we were forced to convert their body size to body mass by an allometric relation between lengths and mass (Andrassy, 1956). The enchytraeids' M was estimated on regression equations of length on fresh weight with the assumption that the ratio of dry weight to fresh weight was 0.18 (Berg *et al.*, 2001). We assume that in presence of a high amount of recorded weights (in our case, more than three thousands), the numerical abundance N of these investigated soil organisms depends allometrically on their average body mass M (regardless life-stage or sex). We checked this conditional expectation by studying the *Studentized residuals* (normal distribution) and by verifying the *linearity* of the average M.

Microbiological samples were collected within the upper 10 cm of soil (same soil sample as for nematodes) and stored one month at a temperature of 12 °C and with a water holding capacity of 50%. The samples for microbial measurements were preincubated at constant conditions to avoid variation caused by weather conditions. Bacterial cells were counted in soil smears by fluorescent staining (5-(4, 6-dichlorotriazin-2-yl)aminofluorescein). Cell numbers, average cell volume, frequency of dividing cells, cell lengths and widths were determined by direct confocal laser scanning microscopy coupled to a fully automatic image analysis system (Bloem *et al.*, 1995a; Paul *et al.*, 1999). To estimate the bacterial biomass from the cell number we used the measured cell volume of the entire bacterial population and a biovolume-to-carbon conversion factor of 3.2 10^{-13} g C μm^{-3} (Bloem *et al.*, 1995b; Van Veen and Paul, 1979). Bacterial cells have an average diameter smaller than 2 µm, with densities of about 2 billion cells per g soil, and a biomass up to 100 kg C ha^{-1}. The extraction of the bacterial community from the soil into a suspension allows its subsequent inoculation (100 µl volume) into a BIOLOG^{TM} multiwell plate for microbial growth measurements (Campbell *et al.*, 2003). The color development in a well indicates the utilization of a specific sole-carbon-source substrate among 31 substrates. The obtained color pattern characterizes the microbial functional diversity.

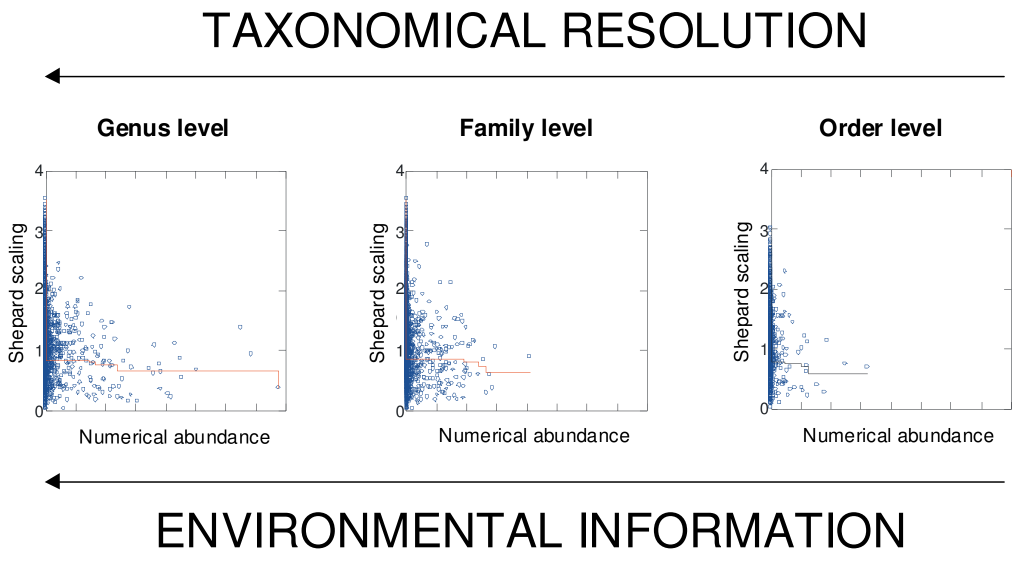


Figure 10. Non-metric multidimensional scaling of the biodiversity at three levels (low: order, intermediate: family; high: genus) of the nematofauna.

Data clustering based on the chord distance of the numerical abundance weighted at taxonomic level (Mulder *et al*., 2000) allows an assessment of the information quality provided by recorded organisms. Discarded products at endemic species level (high scatter) allow for an easy recognition of environmental parameters (Mulder, 1999; Mulder *et al*., 2005).

5.3 Study area

To correlate environmental factors, microbial processes and numerical abundance N of nematodes separately, we used the following Generalized Linear Model (GLM):

$$\log(N) = a + c_1 \times pred_1 + \cdots + c_x \times pred_x + d_1 \times (pred_1)^2 + \cdots + d_x \times (pred_x)^2 + \varepsilon$$

The dependent variable N gave no weight to biodiversity, and considered only $\log_{10}(N)$ kg^{-1} soil weight. The used predictors (*pred.*) were Livestock density (cattle units ha^{-1}), $pH_{(KCl)}$, clay fraction (very fine sediment which is referred to as lutum, particles with a size < 2µm), plant available phosphorus (P), Soil Organic Matter (SOM), rainfall (mm $week^{-1}$) and temperature (no cation exchange capacity and no soil moisture). The GLM results provided a selection of low-pressure, semi-natural farms that were investigated further. Among the low-pressure grasslands detected by GLM, we have chosen two farms: the farm on sand was sampled in 1999, that on river clay in 2002. Both were sampled in the late Spring. The bio-organic farm on sand exhibits a pH of 5.3, lutum 1%, P 640 mg/kg dry soil, SOM 8%, livestock density 1.6 units/ha/year. The conventional farm on clay exhibits a pH of 5, lutum 43%, P 270 mg/kg dry soil, SOM 14% and a slightly lower livestock density (1.4 units/ha/year). These two locations were selected from 124 grasslands on sand and 41 on river clay.

6. Results

Our network offers a sampling infrastructure and closely related chemical measurements that are of vital importance for soil ecological research. So far the database contains samples obtained from dairy farms and several nature areas. Most indicators are significantly different between the investigated soil types and/or land-use forms. Figure 11 shows the extent to what data derived from 70 dairy farms on sandy soils in the Netherlands (grassland soils with a high risk of NO_3^- leaching) provide insight into the effects of management practices on soil fauna composition. The nematological analysis of the occurrence of active bacterial-feeders (*Bf*) shows a highly significant direct correlation of the numerical abundance of *Bf*-nematodes and the plant available P_{org} ($R^2 = 0.37$, $P = 0.0001$). According to Table 3, this result suggests a rapid decomposition and nutrient mineralization (Ingham *et al*., 1985) and a retardation in the vegetation succession (Wardle, 2002; Wardle *et al.,* 2004) under increasing farming intensity. The (relative) dominance of vascular plants with both a higher forage and litter quality (Wardle *et al*., 2004, but see also Van Genderen *et al*., 1997 for organic compounds and Mulder and Ellis, 2000 for inorganic compounds) is further supported by the time series of the nematode Dauerlarvae –the Rhabditida resting stage– on the secondary *y*-axis of Figure 11. The environmental descriptors are here: phosphorus (P_{org}), the sampling period (in weeks), and the mean farm surface (in hectares). The above-ground Net Primary Production (NPP) can not be recognized in the time series of (passive) Dauerlarvae, although the active *Bf*-nematodes strongly suggest increasing litter quality and rapid decomposition (bacterial-based energy channel of the detrital food-web). Especially negative time shifts in the Dauerlarvae reveal increasing litter quality (soil organic matter exhibits $\chi^2 = 580$ and $P < 0.0001$) and suggest easily degradable substrates for the bacteria ($P = 0.0003$). The relative abundance for both the bacterial-feeding (*Bf*) and the hyphal-feeding (*Hf*) habit, respectively, can therefore be seen as a cumulative function of litter quality and quantity. These results strongly indicate that apparently coupled compartments in the detrital food-web share independent detrital-grazing energy channels for bacterial- and hyphal-feeding nematodes. Preliminary results at a national scale are given in Figure 12, where we used the management regime (in this case, livestock density as proxy for above-ground pressure) as environmental descriptor. The ArcMap module (ArcInfo 8) was used to analyze spatial patterns within the nematofauna as predicted at genus level by the livestock density. As the GIS-data frame is a collection of layers (each layer represents a distinct set of physical-geographic features), we modelled the Nematode Channel Ratio as a linear function of livestock units (LSU) according to:

$$\mathrm{NCR} = \left(\frac{Bf}{Bf + Hf} \right) \propto \mathrm{LSU}$$

The whole amount of nematodes (biomass) would be probably sufficient for a rough estimate of the soil productivity in relation to the farming system. However, nematodes are reliable bioindicators, as the small kurtosis of the pH-response of some taxa occurring in Dutch grassland soils supports the importance of a determination at species / genus level (cf. Figure 10). Also the information shown by the nematofauna at functional level can be easily integrated in dynamic models. For instance, the contribution of nematodes to the total abundance of microbivores is more sensitive to the numerical abundance of their bacterial prey than those of other microbivores or micro-detritivores (see Figure 8). Both bacteria and bacterial-feeding nematodes react to the intensity of land management and the kind of farming systems. In fact, the bacterial biomass was highest in organic farms, and lowest at the intensively managed farms (Bloem and Breure, 2003; Mulder *et al.*, 2003b). If we assign the average of the bacterial biomass from organic farms to 100%, conventional, semi-intensive and intensively managed farms differ from the organic farming system respectively by 5, 17 and 19%. Bacterial biomass and standard deviation of the cells were the highest in organic farms (Mulder *et al.*, 2003b). Furthermore, the variation in the average mass of bacterial cells (as derived from the fully-automatized measurement of cell volume) was the highest among the investigated organisms (*Studentized residual* = 3).

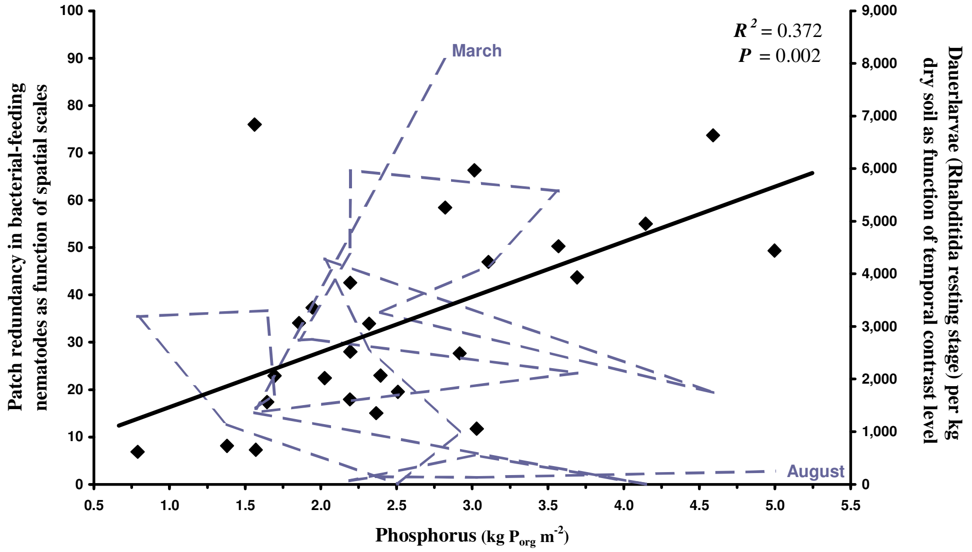


Figure 11. Biplot of active and passive bacterial-feeding nematodes along a nutrient gradient from semi-natural farms (low-pressure) up to intensively managed grasslands. The resting stage of the nematodes is given on the right, as time series from early Spring to late Summer (blue-grey lines).

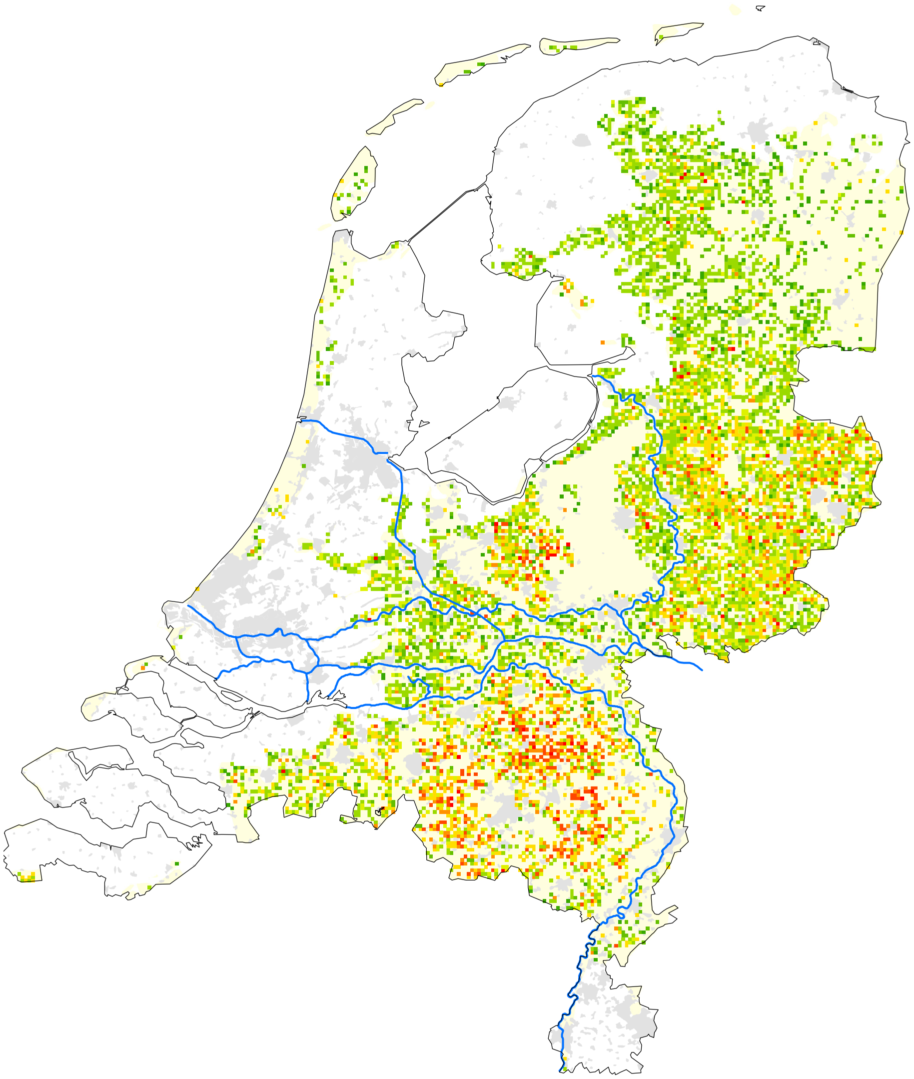
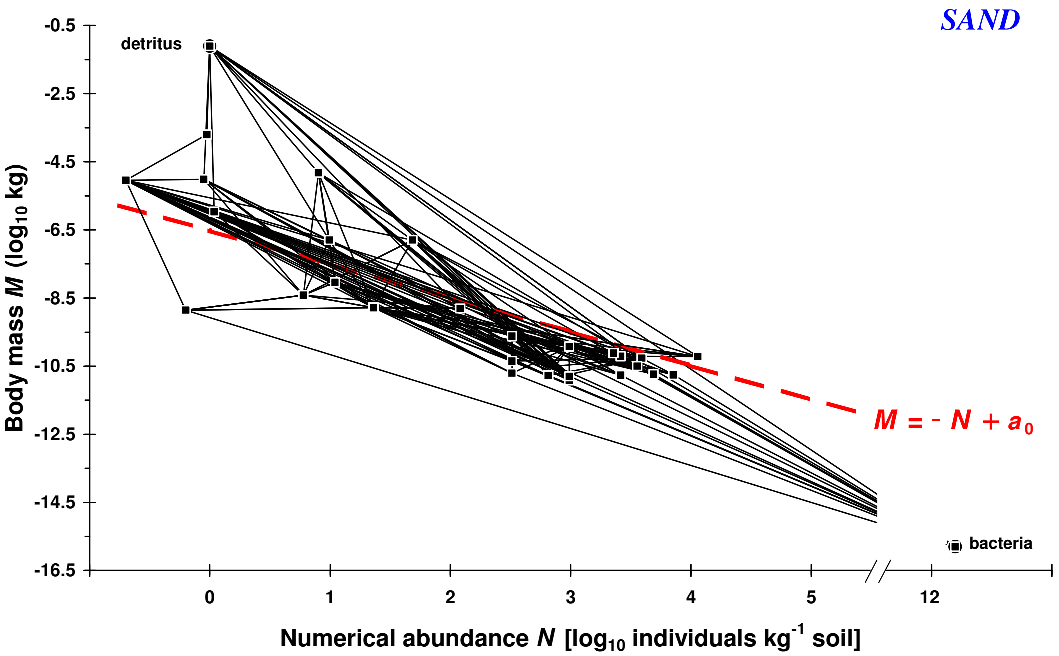


Figure 12. Expected Nematode Channel Ratio (NCR) estimated from the livestock density of grasslands and pastures on sand and river clay

One livestock unit is given here as the amount of dairy cattle excreting 16.1 g N_{tot} m^{-2} $year^{-1}$. The NCR ranges from 0.85 (green pixels, low farming pressure) up to 0.91 (orange pixels, high farming pressure). The nematode distribution in managed grasslands correspond well to the soil resource patterns as defined by the farming regime and the cattle pressure (Mulder *et al.*, 2003b). The NCR average derived from digital metadata at a 1 x 1-km scale equals 0.88.

In Figure 13, we show as ‘reference site’ one bio-organic grassland on sand (upper plot) and another low-pressure grassland on clay (bottom plot). Most species occurring in the soils of these two grasslands fall near a diagonal where the mean slope of the body mass M as function of their numerical abundance N (per kg dry soil) approximates –1, whereas in the case of the organic farm on sandy soils, it equals –1. Such a slope means that a consumer’s total biomass equals its resource’s total biomass (Cohen *et al.,* 2003; Mulder *et al.,* 2005). From our bottom (bacteria) to the upper M-level of decomposers (earthworms), while both M as N increase more than 12 orders of magnitude, their product $B = N \times M$ differs only a factor 2 in sand (from 3.9 10^{-4} kg for bacteria up to 5.7 10^{-4} kg for *Lumbricus*) but two orders of magnitude in clay.
Being greater (less negative) than –1, the slope of the river clay farmyard shows that its consumer biomass abundance increases from the bottom to the top of the food-web. Over all species, B varies only 6 orders of magnitude. In the case of the organic grassland on sand, a slope exactly equal to –1 for the relationship between consumer’s N (dependent variable) and consumer’s M (independent variable) means according to Cohen *et al*. (2003) that one unit of available resource biomass supports a constant (increasing) amount of consumer biomass as the consumer’s M increases. Furthermore, the slope of *each* trophic link indicates the biomass ratio of the two plotted species. A slope of –1 means obviously that consumer $N \times M$ equals resource $N \times M$ (Cohen and Carpenter, 2005; Mulder *et al.*, 2005). In our case, taking the bacterial-feeding nematodes into account, a slope more (or less) negative than –1 indicates that the grazer has greater (or smaller) B, respectively, than the bacterial resource, assuming that the consumer is above and to the left of the resource in Figure 13, as is always the case in this plane. However, in the case of many prey-predator links, this assumption is not entirely true. In our reference grassland on sand, about one fifth of the trophic links show animals preying on organisms with the same body mass or an up to 4 orders of magnitude larger one. Since we have split some orders to a higher taxonomical resolution, predatory mites became evident. Among them, Uropodina are probably the main predators in our reference location on sand (Figure 8). Regardless the amount of taxa that are at the same time grazing on bacteria and feeding on detritus (i.e. dead plant material/fungal mycelium), both the slopes of the regression lines of the estimates of M on N (Figure 13) and N on M remain extremely significant ($P < 0.0001$). Merging at taxonomic level do not introduce statistical biases: mean weight and standard deviation show the same variation patterns for predatory as for non-predatory species. Body mass is determinant for spatially-scaled predatory activity, for interaction strengths between predator and prey, and for the link structure in any food-web. Our predators are usually 1-5 orders of magnitude larger than their prey, in terms of average body mass, while our microbial grazers are 5-10 orders of magnitude larger than their prey, in terms of average mass of bacterial cells. However, the situation within the microbial community is different, as we are forced to lump together many different bacterial species (Mulder *et al.*, 2005).



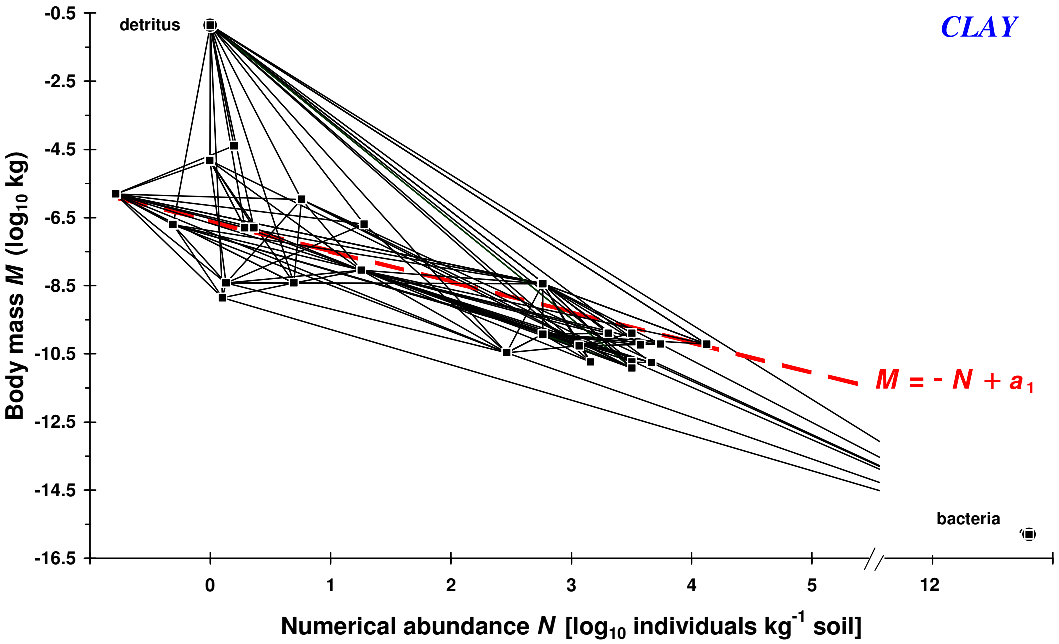


Figure 13. Two plots depicting all below-ground interactions that take place in one soil food-web between all taxa, in four trophic levels, with two basal resources, at any time of the year, and in response to all possible environmental shifts the land-use management may cause in the field over time.

Numerical abundance *N* (individuals per kg dry soil) and average body mass *M* of soil organisms in two organic/conventional farms in the Netherlands. Double logarithmical scale, all logarithms calculated with base 10. The upper figure represents the scatter at genus level of all organisms occurring in a sandy soil, the lower shows one analogue scatter for the community of river clay soil. In both cases, the diagonal slope for all soil organisms approximates –1 (exactly 135° for sand and a slight difference, 138°, for clay soil). The *M*-intercepts (on their $\log_{10}$ scale) differ even less than their slopes ($a_0 = -6.5$; $a_1 = -6.6$).

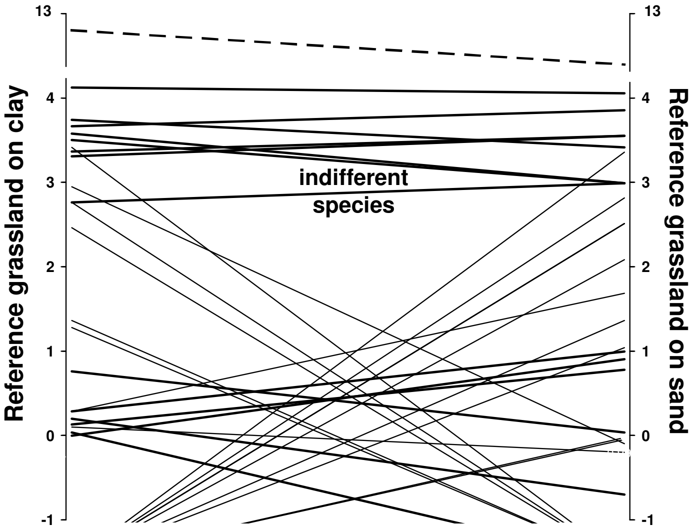


Figure 14. Bipartite graphs depicting two-node networks characteristic of the relative occurrence of soil organisms plotted in Figure 13.

The numerical abundance *N* has been log-transformed (broken vertical axis below the bacteria). Note that some taxa reach negative *N* values (less than one individual per kg soil). Many of these taxa are selective (see Table 4 for more details). Most nematodes fall within the basal fauna (stress tolerant and indifferent, present in almost all soils). Thin oblique lines represent characterizing soil organisms, thick lines –regardless their abundance– companion species with a fluctuation less than one order of magnitude. Accidental species have not been taken into account in this numerical analysis.

The existence of different patterns among and between detrital food-webs in our grassland is in agreement with functional differences at higher trophic levels between species-poor and species-rich ecosystems (Spencer *et al.*, 1999) and with the complementarity action of energy transfer agents (small organisms with $M < 0.25$ µg) *vs* habitat engineer agents (large organisms with $M > 15$ µg, like the lumbricids). The physical structure of soils (for instance, lutum-filled pores) contributes to explain further the much lower numerical abundance of larger predators in a clay soil in comparison to a sandy soil (Figure 13 and Table 4). Notwithstanding the difference in resources between these two soils (the detritus *M* and the bacterial *N* in clay-rich soil are more than 2-fold than in sandy soils), effects of a different management regime and land use can be easily recognized comparing the functional ecology of the soil organisms of our bio-organic farms on sand (top Table 5, $n = 10$) with our semi-natural, low-pressure farms on river clay (bottom Table 5, $n = 18$). An evident example is provided in Table 5 for river clay, where the bulb mite *Rhizoglyphus*, elsewhere regarded as pest (Radwan and Bogacz, 2000; Díaz *et al.*, 2000), occupies as selective species an important niche of the soil food-web. Moreover, in absence of competitive fungivore organisms, like hyphal-feeding nematodes, springtails become selective or even preferential species, like those belonging to the *Isotoma*-group (*Isotomiella minor*, *Isotomurus palustris*) and –on sandy soils– *Hypogastrura*. As the numerical abundance of hyphal-feeding nematodes differs one order of magnitude from that of bacterial-feeding nematodes (Table 5), fungivore collembolans occupy an important role in the litter. Actually, micro-arthropods play a key-role in the structure of the food-webs in Figure 13, as can be seen by the rapid increase of the predators' *N* (general predators and predators of arthropods). There is an evident shift among arthropod functional groups. Although engulfing fungivores (collembolans that ingest mostly hyphal branches and fungal spores) are spread over both soils, Prostigmata (predating mites that attack arthropods and/or nematodes) and Mesostigmata (general predators) comprise mostly selective species (Table 4). The enchytraeids, often regarded as essential decomposers in the (surface and root) litter, fluctuate in our organic farms on sand only by a factor of 4.

Table 4. Characterizing soil organisms of our two reference grasslands (Figure 13) with their biomass (g/kg). The upper part depicts characterizing below-ground organisms with their biomass (i.e., numerical abundance times their –fixed– body mass) for a sand community, the lower part depicts a river clay community.

	Sand	River clay
Histiostoma (Astigmata)	$8.8\cdot10^{-7}$	$1.8\cdot10^{-6}$
Scutacaridae (Prostigmata)	$2.3\cdot10^{-5}$	$5.1\cdot10^{-6}$
Dolichodoridae (Nematoda)	$8.9\cdot10^{-5}$	$2.6\cdot10^{-5}$
Alliphis (Mesostigmata)	$9.9\cdot10^{-5}$	
Dauerlarvae (Nematoda: Rhadbidita)	$1.7\cdot10^{-4}$	
Dorylaimidae (Nematoda)	$2.1\cdot10^{-4}$	$6.3\cdot10^{-5}$
Enchytraeus (Enchytraeidae)	$7.7\cdot10^{-3}$	$3.1\cdot10^{-4}$
Hypogastrura (Collembola)	$8.7\cdot10^{-3}$	
Sminthurinus (Collembola)	$1.2\cdot10^{-1}$	$1.5\cdot10^{-2}$
Lumbricus rubellus (Lumbricidae)	$1.9\cdot10^{-1}$	
Paratylenchidae (Nematoda)	$1.2\cdot10^{-5}$	$3.9\cdot10^{-5}$
Aphelenchoididae (Nematoda)	$1.8\cdot10^{-5}$	$5.8\cdot10^{-5}$
Pratylenchus (Nematoda)		$2.2\cdot10^{-4}$
Bdella (Prostigmata)		$2.6\cdot10^{-4}$
Rhabditidae (Nematoda)	$1.6\cdot10^{-4}$	$3.4\cdot10^{-4}$
Aporcelaimellus (Nematoda)		$2.1\cdot10^{-3}$
Rhizoglyphus (Astigmata)		$3.8\cdot10^{-3}$
Isotoma (Collembola)	$1.2\cdot10^{-3}$	$6.2\cdot10^{-3}$
Dendrolaelaps (Mesostigmata)		$8.0\cdot10^{-3}$
Aporrectodea caliginosa (Lumbricidae)		$6.3\cdot10^{-2}$

Taxa found most frequently in one soil but rarely in both are SELECTIVE SPECIES (e.g., *Alliphis*, *Bdella*, *Dendrolaelaps*, *Pratylenchus*, *Rhizoglyphus*); taxa present in several farms more or less abundantly but with a greater deal of vigour in one soil type are defined as PREFERENTIAL SPECIES (Aphelenchoididae, Rhabditidae, etc.); taxa without a definite affinity for any particular soil are defined as INDIFFERENT SPECIES (ranking according to Braun-Blanquet, 1951). Please compare the trends with the bipartite graph of Figure 14.

Table 5. Functional guilds in sandy soils (upper part, bio-organic grasslands sampled in 1999, n = 10) and river clay (lower part, semi-natural grasslands sampled in 2002, n = 18).

	Reference	**Functional guilds (m^{-2})**	**Minimum**	**Average**	**Maximum**
SAND		**Nematodes**			
	$1.6\cdot10^{5}$	Hyphal feeders	0	$1.6\cdot10^{5}$	$3.2\cdot10^{5}$
	$1.4\cdot10^{6}$	Bacterial feeders	$8.2\cdot10^{5}$	$1.6\cdot10^{6}$	$2.6\cdot10^{6}$
	$3.1\cdot10^{5}$	Predators/omnivores	$1.0\cdot10^{5}$	$3.2\cdot10^{5}$	$5.3\cdot10^{5}$
	$1.8\cdot10^{6}$	Plant feeders	$1.2\cdot10^{6}$	$2.3\cdot10^{6}$	$4.8\cdot10^{6}$
		Micro-arthropods			
	$9.5\cdot10^{2}$	Predators of arthropods	0	$3.2\cdot10^{2}$	$1.3\cdot10^{3}$
	$1.7\cdot10^{3}$	Predators of nematodes	0	$1.2\cdot10^{3}$	$4.9\cdot10^{3}$
	$3.4\cdot10^{3}$	General predators	$1.7\cdot10^{3}$	$4.1\cdot10^{3}$	$9.9\cdot10^{3}$
	$8.4\cdot10^{3}$	Panphytophagous	$1.6\cdot10^{3}$	$3.5\cdot10^{3}$	$2.6\cdot10^{4}$
	$2.2\cdot10^{3}$	Omnivores	$2.8\cdot10^{2}$	$3.3\cdot10^{3}$	$8.6\cdot10^{3}$
	$9.5\cdot10^{1}$	Bacterivores	0	$1.9\cdot10^{1}$	$9.5\cdot10^{1}$
	$8.7\cdot10^{4}$	**Enchytraeids**	$1.8\cdot10^{4}$	$4.1\cdot10^{4}$	$8.7\cdot10^{4}$
	$1.7\cdot10^{2}$	**Lumbricids**	$7.5\cdot10^{1}$	$2.5\cdot10^{2}$	$4.5\cdot10^{2}$
RIVER CLAY		**Nematodes**			
	$2.6\cdot10^{5}$	Hyphal feeders	$1.2\cdot10^{4}$	$1.2\cdot10^{5}$	$2.6\cdot10^{5}$
	$1.0\cdot10^{6}$	Bacterial feeders	$3.7\cdot10^{5}$	$7.3\cdot10^{5}$	$1.2\cdot10^{6}$
	$2.1\cdot10^{5}$	Predators/omnivores	$8.0\cdot10^{4}$	$1.8\cdot10^{5}$	$2.7\cdot10^{5}$
	$2.0\cdot10^{6}$	Plant feeders	$8.4\cdot10^{5}$	$1.6\cdot10^{6}$	$2.9\cdot10^{6}$
		Micro-arthropods			
	$3.8\cdot10^{2}$	Predators of arthropods	0	$2.7\cdot10^{2}$	$1.2\cdot10^{3}$
	0	Predators of nematodes	0	$1.0\cdot10^{3}$	$6.1\cdot10^{3}$
	$1.9\cdot10^{3}$	General predators	$3.8\cdot10^{2}$	$7.9\cdot10^{2}$	$7.2\cdot10^{3}$
	$1.0\cdot10^{4}$	Panphytophagous	$1.5\cdot10^{3}$	$5.7\cdot10^{3}$	$3.4\cdot10^{4}$
	$5.7\cdot10^{2}$	Omnivores	0	$1.2\cdot10^{3}$	$4.2\cdot10^{3}$
	$3.8\cdot10^{2}$	Bacterivores	$3.8\cdot10^{2}$	$5.6\cdot10^{2}$	$4.2\cdot10^{3}$
	$3.1\cdot10^{4}$	**Enchytraeids**		NA	
	$1.3\cdot10^{2}$	**Lumbricids**	$3.9\cdot10^{1}$	$8.8\cdot10^{1}$	$1.7\cdot10^{2}$

The numerical abundances of soil animals are given as counted individuals per square meter (Minimum, Average and Maximum values). The reference values on the left are those for the two locations plotted in Figure 13. NA = not available yet (complete enchytraeids' dataset ready only for sandy soils). For bacteria see Table 6.

Table 6. Ecophysiological traits of the bacterial population occurring in the same sandy soils (n = 10) and clay-rich soils (n = 18) as in Table 5.

	Reference	**Ecophysiological traits**	**Minimum**	**Average**	**Maximum**
SAND	$2.5\cdot10^{9}$	Bacterial cells (g^{-1})	$6.5\cdot10^{8}$	$2.3\cdot10^{9}$	$5.5\cdot10^{9}$
	0.22	Bacterial volume (μm^3)	0.19	0.22	0.25
	63	DNA banding patterns	37	49	63
	79	C mineralization rate	28	62	90
	9	N mineralization rate	6	10	14
	0.90	Respiratory Quotient	0.63	1.31	4.81
	$4.4\cdot10^{7}$	Colony-Forming-Units	$1.5\cdot10^{7}$	$3.5\cdot10^{7}$	$5.1\cdot10^{7}$
	0.76	BIOLOG^{TM} Hill slope	0.41	0.59	0.76
RIVER CLAY	$6.4\cdot10^{9}$	Bacteria cells (g^{-1})	$3.1\cdot10^{8}$	$2.8\cdot10^{9}$	$6.5\cdot10^{9}$
	0.27	Bacterial volume (μm^3)	0.23	0.27	0.32
	66	DNA banding patterns	53	62	73
	136	C mineralization rate	26	77	136
	6	N mineralization rate	1	4	8
	1.18	Respiratory Quotient	0.87	1.29	3.59
	$5.8\cdot10^{7}$	Colony-Forming-Units	$8.3\cdot10^{6}$	$9.5\cdot10^{7}$	$8.7\cdot10^{8}$
	0.38	BIOLOG^{TM} Hill slope	0.30	0.44	0.71

The numerical abundance of bacterial cells in one gram dry soil is the average of two pseudoreplica's per location, whereas the bacterial volume provides the average volume per bacterial cell. The *potential* C and N mineralization rates under standardized conditions in the laboratory are proxies for microbial activity and are given in mg kg^{-1} $week^{-1}$. To merge the CO_2 production with the O_2 consumption, we used the Respiratory Quotient, the ratio of the mol CO_2-evolution (basal respiration) per mol O_2-uptake.

The characteristics and microbial activities of the bacterial population is given in Table 6, for the same locations as in Table 5. Clay shows a remarkable higher amount of bacterial cells than sand (Table 4; cf. Bloem and Breure, 2003), a higher number of DNA bans and much more Colony-Forming-Units (CFU) on agar. Table 6 shows other relevant ecophysiological traits of bacteria in our soils in the form of substrate utilization patterns. The BIOLOG^{TM} microtiter plate for sole-carbon-source test allows a further investigation on the soil microbial communities. Using these multiwell plates, it becomes possible to produce metabolic fingerprinting, or so called community-level physiological profiles (CLPP) of a particular ecosystem. These profiles give insight into the metabolic composition of the microbial community, which is equivalent to the information from classical ecological field observations about species abundance and composition. From the CLPP of many soil and reference samples, it was observed that environmental stress (like pollution or intensive agricultural practices) affected the autochthonous microbial communities, but the ecological significance of these changes has to be investigated. Taking the slope of a linear fit of the log-normal distribution of the average well color development (AWCD) of a BIOLOG^{TM} ECO-plate into account, we see that in our reference location on sand the fitting line at the inflexion point of the observed AWCD-values on $\log_{10}$(CFU/ml) are much steeper. The physiological response of soil microbiota measured by the Respiratory Quotient shows in our reference location on sand a two times higher ratio of CO_2-evolution per mol O_2-uptake than in our clay location. Again, if we would be able to distinguished bacteria into more specific (taxonomically narrower) groups, the numerical abundance of each group would be much smaller and the data point would be replaced by a group of data points lying to the left of the present data point for all bacteria combined. Thus, by distinguishing taxonomically among the bacteria, we may narrow a straight line plot. At functional level, colony forming units (CFU) provide some way of estimating the taxonomic diversity of bacteria and the different species or other taxonomic groups in a sample. However, further microbiological investigation is necessary. At this point we prefer to plot bacteria as one point, giving its resource characteristics (exactly as with detritus).

The separate energy pathways of the bacterial and fungal channels in soil ecosystems may provide increased dynamic stability when simultaneously linked to the same microbi-detritivore consumers (Mulder *et al.*, 2003; Yeates, 2003). On the contrary, with respect to more complex food-webs, separate energy pathways (see Figure 5) imply that arthropod predators feed off varying food-web compartments at lower trophic levels at different points in time, thus temporarily linking them into the larger food-web of the surface litter (O'Connell and Bolger, 1997) reported significant differences among microphytophages and predators in consuming/predating efficiency). However, if the results obtained for food chains can be transferred to more complex terrestrial food-webs, i.e. if top predators of complex food-webs gain dynamic stability from switching between food-web compartments, remains to be demonstrated (Brose *et al.*, 2005). These implications include that (1) soil organism necessitate a certain soil structure, (2) species operate therefore at different spatial scales, (3) some species, e.g. top predators of large body size, being likely to be distributed across and temporally integrate local food-webs. Differences between potential (all trophic links of Figure 8) and realized food-webs (field reality) imply that the food-web structure in local soil habitat patches (expressed as slope and/or as intercept) reflects population dynamics and resource availability in space and time.

7. Discussion

As many ecosystem services fundamental to life are provided by small (almost neglected) soil organisms, environmental scientists are faced with a difficult task. Can these scientists calculate the value of a natural resource, seen that their critical answers have to provide the very-basic information for management strategy and policy? There are different benefits and services to price. Land products are always easy to quantify directly. The economical evaluation of *services* is more difficult, but still feasible. For instance, we may easily calculate the costs of *neglected services* as costs-benefits (like water purification in the coastal dunes). Much harder is the economical evaluation of recreational or even aesthetic benefits, as not everyone agrees with physical planning and urban development. Actually, most practical problems for policy makers are the extremely differing philosophical bases of the public and farmers involved.

Until now, most tentative approaches focused merely on bioindicators. For instance, the fungi-to-bacteria ratio is supposed to be a valuable number to infer ecological soil quality. On the other hand, nematodes and earthworms are both present in high numbers, show a high species diversity, and are also easy to count. Their numerical abundance provides good information of the diversity and stability of the below-ground soil ecosystem. However, we have to take into account that –notwithstanding the key-role of earthworms for the soil structure is well-known by farmers and nature conservationists (earthworms are the main food source for many above-ground living animals like birds, badger, etc.)– most farmers still associate nematodes with plant-parasitic pathogens. Thus nematodes are not appealing (yet) to farmers, earthworms are.

To a certain extent, the recognition of the importance of free-living nematodes for the processes occurring in soil ecosystems started with Yeates (1979). For example, nematodes cover several trophic levels by feeding on algae and higher plants, on bacteria and fungi, or on soil animals (in particular other nematodes), thus being a central (and diverse) element of the soil food-web (Ekschmitt *et al*., 1999; Yeates and Bongers, 1999). Especially the cycling of nutrients in the soil is controlled by nematodes, mainly by stimulating microbial growth when feeding on them. In addition, they influence the dispersal of microorganisms, act as food source for many other organisms (like predatory mites) and, despite some species being pathogenic themselves, provide a biological control of parasites and other pests. Seen the numerical abundance and body mass of soil nematodes (Figure 8), they affect together with detritus and bacteria the slope of the regression line in a very significant way. The nematofauna incorporates most species feeding on microflora, and play therefore a key-role in energy fluxes. Higher taxonomic groups, like collembolans, enchytraeids, and earthworms, show a marked preference for dead organic matter (primary decomposers). Aside oribatids, secondary decomposers feeding on bacteria and nematodes, other mites belong often to the first and second predatory level. For instance, *Pyemotes* includes a wide morphological variety of insect parasites (Cross and Moser, 1975). These bee mites are natural enemies of insects and may play – although pests in apiculture– an important role in biological control (Krczal, 1957; Cross *et al.*, 1981), like other predatory mites preying on larvae of insects that become as adults a pest problem (Enkegaard *et al.*, 1997). In contrast to 'pure food-webs', which do not take into account mutualistic interactions basic for ecosystem services like pollination and seed dispersal, parasitism and oviposition have been taken into account in Figure 8 as biological link (i.e., trophic link in a life-stage or generation).

There have been few studies describing the actual impact of grazing cattle on the abundance and biodiversity of soil fauna. Effects of environmental stress on the litter and soil fauna related to increasing stocking intensity have been recognized –among others– by King *et al.* (1976) in the springtails' community, by Kay *et al.* (1999) in the mite assemblages and by Mulder *et al.* (2003b) in the nematofauna. In particular the last two authors found that the numerical abundance of microbivores (for mites, those belonging to the families Nanorchestidae, Tarsonemidae and Tydeidae; for nematodes, both the active bacterial-feeders as the hyphal-feeders) declined with livestock intensity and were much lower in grazed compared with exclosed grasslands.

A scenario in which intensified agricultural land use is foreseen might show that Life Support Functions (LSF) will still exist but will be less sustainable, which might be due, for example, to reductions in the number of species in functional groups. A functional group is a group of related organisms that perform the same function in an ecosystem, e.g. nitrogen-fixing bacteria, or bacterial-feeding nematodes. On the other hand, if action were sought to maximize sustainability, the number of species executing certain tasks within functional groups would have to be maximized (cf. Heemsbergen *et al.*, 2004; Mulder *et al.*, 2005), which would generate critical limits on various land-use parameters in relation to the conservation of biodiversity.

Seen increasing cattle pressure as predictor for anthropogenic reductions in soil biodiversity, we may expect in our narrow future increasing phase shifts (Scheffer *et al.*, 2001). In such a scenario, shift rapidity has to be seen as the result of ecosystems with an inherently low biodiversity. Decreased species diversity within functional groups (e.g., Cohen and Newman, 1988; Naeem *et al.*, 1994; Tilman, 1996; McGrady-Steed and Morin, 2000; Mulder *et al.*, 2003b, 2005) destabilize ecosystems. Declines in the species that are characterizing strong interactions between trophic levels result obviously in trophic-level dysfunction.

The arising issue remains the stability of food-webs. In his detailed review of over 100 allometric regressions on metabolic rate, age and numerical abundance, Hendriks (1999) noted that the variation in the correlation coefficients of the regressions on density is much higher than those on age (and obviously rate, as the reciprocal rate and age parameters are expected to be equal but of opposite sign). Seen furthermore that the numerical abundance of taxa with a given body size may be in aquatic environments more than one order of magnitude higher than equally sized taxa in terrestrial habitats (Hendriks, 1999), the literature focus on aquatic food-webs is understandable. However, despite their still high numerical abundance and species richness, soil organisms with a body size less than 1 mm are poorly represented in most published food-webs (Woodward *et al*., 2005). Actually, very few studies include data from the entire community size spectrum. At the functional group level, long trophic loops containing a relative high number of weak links are known to increase stability (Neutel *et al*., 2002). However, a similar stability in the distribution of consumer-resource interaction strengths is affected by a high spatial heterogeneity. Being any community food-web linked to an arbitrary spatial definition, the monitoring of smaller organisms (i.e., soil animals restricted to microhabitat patches) can deeply affect the definition (and subsequently, the evaluation) of the whole investigated habitat. Such conclusions are supported by previous models of Cousins (1980, 1987a, 1996). In fact, he pointed out that it is the variation in *body sizes* (and related territory of either a consumer or a predator) the key parameter for any organism within a food-web (cf. Cohen and Briand, 1984 and Cohen *et al*., 1993b), not its non-integer trophic level or its fixed taxonomy. Many authors have had strong criticism on taxonomy, although most of them do not consider that nomenclature often relies on *the same* morphological character states that they use to define the functional ecology within their models. For instance, in the case of plants, Linné (1784) used the structure and the smell of the flower to describe (and provide a name to) species, whereas exactly the same attractors determine the plant-animal interactions. Bongers (1994) often used the adult body mass and the buccal cavity of nematodes to correlate a taxon with its life-strategy, Yeates *et al*. (1993) to infer its feeding habits. This integrated approach causes a certain overlap among disciplines.

As physiological rates like production/excretion and mortality can be seen as function of body size in both aquatic as terrestrial ecosystems (extensive review in Peters, 1983; further results described in Cyr *et al*., 1997; Petersen, 1981; and West *et al*., 2004 for collembolans –soil interface–, plancton –lake surface–, and birds, respectively), differences in the relationships between numerical abundance and body size have large implications for ecosystem functioning. To our knowledge, most studies of local communities are focused on taxonomically related species which often span a narrow range of body size.

We believe that the integration of numerical abundance and body size in one diagram (Figures 8 and 13) provides the possibility to link at the same time the character states of the investigated soil organisms (a) to their morphology (taxonomy), (b) to their resource/prey, and (c) to their relative energy use. In the case of the resources, it should be taken into account that we do not use the term detritus as only dead organic matter, but include 'dying plant tissues' as proposed by Petersen and Luxton (1982). This detail is crucial, as fine root production (and correlated mycorrhizal fungi) deeply affect the biomass, production and respiration of the microflora (Petersen, 1995; Hokka *et al*., 2004). Regardless the kind of above-ground vegetation, the availability of derived resources is always a *conditio sine qua non*. Resources are in fact patchy and vary in space and time. An obvious conclusion is that the spatial structure of the environment is *always* determinant for predators (Cousins, 1987b), invasive species (Sakai *et al*., 2001), trophic interactions (Brose *et al*., 2005), communities (Chust *et al*., 2003a), or ecosystem functioning (Bengtsson *et al*., 2002).

The physical importance of the *ecosystem spatial structure* for recovery from stress is striking if compared with the weak observed relationships between faunal recovery and environmental disturbance in laboratory microcosm experiments (e.g., Liiri *et al*., 2002; Salminen *et al*., 2002; Van Gestel and Koolhaas, 2004). From this perspective, it becomes clear that the most widespread mechanism occurring among consumer-prey interactions is a certain functional equivalence across trophic levels. In our soil ecosystems, the switch that occurs between Figure 15b and 15c is related, to a certain extent, to the body size of the consumers/predators. However, the decrease in the biodiversity of microbivores under specific environmental conditions can be easily pointed out by comparing the links between bacteria and bacterivores in our two food-web diagrams. In fact, the density of the trophic links across a soil community in sand is much higher than those in a clay-rich soil, where soil pores are frequently filled by lutum. This means that soil pore size and numerical abundance of organisms play a key-role in defining the population structures and ecology of the detrital food-web. It does this by limiting movements and access of some larger-sized animal groups, to all or part of their (bacterial) prey, as well as by supplying living space acting as refuges from predators for other animal groups (or life stages, like Dauerlarvae).

The actual influence of body size of soil organisms on the *nutrient dynamics* in agroecosystems is probably low, at least at top predator level, suggesting a widespread dominance of interactions occurring at the bottom of detrital food-webs and confirms previous results (cf. Setälä *et al*., 1996 and Bongers *et al*., 1997). The density of trophic links, the intercept (due to the direct relation of detritus to primary productivity) and the slope enable us (1) to recognize actual differences in the ecosystem functioning and (2) to evaluate the ecological services under specific environmental conditions (Table 7).

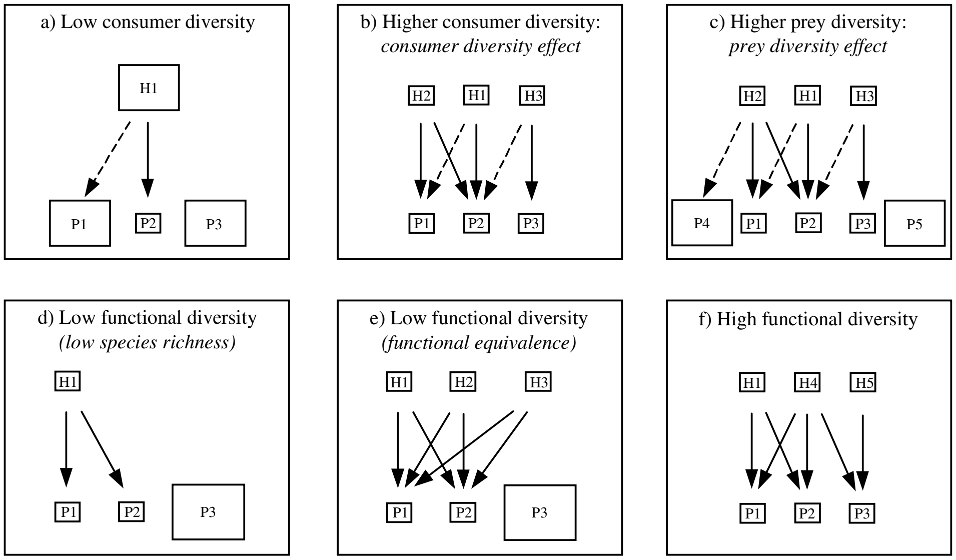


Figure 15. Functional diversity in trophic interactions as reviewed by Duffy (2002).

Above: (a) Low consumer diversity, higher prey diversity (feeding preference). (b) Higher consumer diversity, enhanced impact on prey. (c) Higher consumer diversity, high prey diversity. Below: (d) Low consumer species richness. (e) All consumer species fed on the same resource. (f) Different consumer species having strong impact on their prey (P).

Table 7. Ecological services and coupled parameters under low pollution rates (Breure et al., 2003b).

	Direct nutrient availability	*Soil structure / texture*	*Upper water percolation*	*Clean ground-water*	*Clean freatic water*	*Pests and diseases in agriculture*	*Land-use change-ability*	*Ecosystem resilience / resistance*
Grasslands / pastures	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**
Arable fields	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**
Recreation and nature	**X**	**X**	**X**	**X**	**X**			**X**
Recreation potential (national)	**X**	**X**	**X**	**X**	**X**			**X**
Recreation / housing (urban)	**X**	**X**	**X**	**X**			**X**	**X**
Physical planning (edified)		**X**	**X**	**X**				

Box 2. Microbi-detritivores like nematodes and earthworms are both present in high numbers, show a high species diversity, and are also easy to count. Although nematodes and earthworms provide a rough estimate of below-ground soil quality (Brussaard *et al*., 1997), only microbiological patterns of substrate utilization would contribute to discriminate further between different locations. Alas, routine microbial techniques for the investigation of independent bacterial communities within a given location are not allowable yet. Laboratory experiments are the most easily conducted, but are difficult to extrapolate meaningfully to the field. Using mathematical evidence derived from field studies, a hypothesis is formulated to explain how below-ground microbivores (soil nematodes and litter micro-arthropods) may become affected by gradually increasing effects of land management and this is discussed in relation to defining "critical" conditions for ecosystem sustainability in agricultural soils. In fact, the nematofauna incorporates most species feeding on bacteria and play therefore a key-role in non-forested ecosystems. The constant energy fluxes can be derived from the slope of the regression for a complete soil community. These slopes measure the relative occurrence of small (microfauna) to large species (macrofauna) in relation to their resources, and tend to be more steeply negative in highly productive intensive farming systems with a low bacterial population (unsustainable farming conditions).

8. Conclusions

Agroecosystems in the Netherlands are heavily fertilized and patchy. Management practices like high stocking density cause shifts in functional groups of soil organisms and affect the nutrient dynamics of the soil. Although it is commonly accepted that a biome represents a large but still homogeneous unit of the biotic and abiotic components on Earth, various terms have been used to describe areas for extensive comparison. Natural selection and self-organization jointly interact as a new way to view the evolution of ecological systems (Levin, 1999). The odd notion of equilibrium embedded in Lotka-Volterra equations moved to nested sets of cycles of adaptive change covering spatial patterns and temporal trends (Holling, 1973, 1986, 1992), then to that of multistable states (Carpenter, 2000), and finally to cascade up scales, with fast events affecting slow ones (Holling *et al.*, 2002).

Until now, considerations of yield forced a focus on *suitability* of soils for agriculture. Land-use and soil characteristics became therefore strictly correlated and increasing costs might lower short-term benefits. On the other hand, a *sustainable* agroecosystem under a specific farming regime can be derived from increased quality of ecological services, like direct nutrient availability, water percolation, and less pest and diseases in agriculture. The quality (*suitability*) and stability (*sustainability*) of the soil ecosystem has to be monitored and modelled carefully to keep an environment as long as possible in the future. Soil biodiversity is regarded as useful indicator for soil quality, but the taxonomic and the functional diversity are affected by increasing farming pressure (cattle density, liming, pesticides and other pollutants) in different ways. The actual difference between a list of species that have to be preserved (taxonomic diversity) and an assemblage of soil organisms with specific tasks and duties (functional diversity) is a main goal for the choice of management practices. Appropriate forms of sustainable management can be kept efficient at different spatial scales, from local (by the farmer himself), up to regional (national government) and even continental (European Union). Sustainability means that – notwithstanding a narrow correlation of soil characteristics and suitable land-use due to the recent history of our landscape– the biotic parameters of any soil community (precise richness, autogeneous dynamics, etc.) remain criteria for soil quality (Van de Leemkule, 2001).

Ecological modelling suggests that a strong, selective, man-induced pressure is acting on most taxa, indicating decreasing resilience. We sought explicitly to test for relationships between the absolute numerical abundance N of bacterial cells and soil organisms (nematodes, mites, collembolans, enchytraeids and lumbricids) under different land-management. Decreasing population rates within different trophic groups were sufficiently robust to encompass management regimes and soil types. A selected focus on the first five orders of magnitude of *N* allows already a detailed vision of the occurring trophic links in the soil micro-, meso- and macrofauna.

Our results enable us to show the structure of the trophic links between resources (bacterial population and dead detritus) and terrestrial fauna occurring under a given farming system in a certain soil. Slopes of regression lines close to –1 suggest great resistance and resilience of the food-webs. For instance, we can see that the numerical abundance of bacterial cells under organic and conventional grasslands is strictly correlated with the application of farmyard manure. On the other hand, the numerical abundance of earthworms decreases slightly with management intensity and also the relative amount of epigeic species decreases, indicating variations in: i) porosity in the top layer of the soil and ii) litter quality and related nutrient turnover. Although more resources (bacteria and detritus, higher turn-over) contribute to a different intercept, for both nutrient-rich as nutrient-poor environments the only slope which states a dynamic equilibrium between the bacterial population, the microbial grazers and their predators equals –1, making this assessment extremely reliable for our purposes.

The goal of this paper is to propose some simple graphical and quantitative indicators of community composition and function in soil communities, and to illustrate the application of these indicators to farmed Dutch grasslands on sand and clay. These indicators are potentially useful to show how soil communities respond to different farming practices. We find that these new indicators are superior to previous indicators of ecosystem functioning in the following respects:

- The slope and the intercept provide a common currency to measure ecosystem functioning by a comparison of the links between different ecosystem components and enable us to express feedback loops at both the taxonomic or ecosystem level.

- As the slope is driven by bacteria and organic matter (resources), the integration of all biotic parts in one figure for the characterization of multiple, fluctuating states according to the intensity of land-use is highly desiderable.

As most ecological services are regarded as falling outside market economics, an ecological model that enables the estimation of the occurrence of a given organism of a certain body size offers encouraging opportunities for monitoring and quality assessment of open landscapes. Both the Dutch as the European jurisdiction on physical planning shows a compulsory role of conservation ecology and biodiversity policy in decision-making and legislation. However, most policies simply require a so-called *Red-List* of targets for legal conservation status. We believe that our structural approach contributes towards an extensive comparison of agroecosystems.

Box 3. The Dutch Soil Quality Network offers a sampling infrastructure for abiotic and biotic measurements. Our network allows the recognition in the soil biota of both categorical effects –effects due to different management regimes, i.e. bio-organic, bio-dynamic, conventional, semi-intensive and intensive farming– as quantitative effects, for instance ecological shifts in the functional ecology of soil organisms under increasing livestock density. Any interpretation of ecological shifts requires a ‘reference’. The relationships between the numerical abundance of soil organisms and their body mass allows to asses the extent to what the linear regression for the whole soil community narrows –1 (–45 degrees). Such a value for the slope of the regression line imply the most efficient ecosystem functioning possible for one soil under a given management regime, thus its Life Support Functions may be set at 100%. Under ‘stable conditions’, cattle, grasses, and a host of soil organisms ranging from earthworms and mesofauna (mites, collembolans, enchytraeids and nematodes) to microflora (bacteria and fungi) interact in ways beneficial to each other. Moreover, the more ‘self-organizing’ the ecosystem (thus, the more *DYNAMICALLY STABLE* its detrital food-web), the fewer feed-backs need to be introduced by managers. Most interactions across the detrital food-web should not really be described only as species competition, as the resulting biomass production of soil organisms (and consequently carbon and nitrogen drawdown) improves detritus and litter quality (and consequently the soil fertility and the crown/root components of palatable grasses).

References

Andrassy, I., 1956. Die Rauminhalts- und Gewichtsbestimmung der Fadenwürmer (Nematoden). Acta Zool. Hung. Acad. Sci. 2, 1–15.

Bakker, J.P., 1989. Nature Management by Cutting and Grazing. Kluwer: Dordrecht.

Beerling, D.J., Woodward, F.I., 2001. Vegetation and the Terrestrial Carbon Cycle: Modelling the first 400 million years. Cambridge University Press: Cambridge.

Bengtsson, J., Engelhardt, P., *et al.*, 2002. Slippin' and slidin' between the scales: the scaling components of biodiversity-ecosystem functioning relations. In: Loreau, M., Naeem, S., Inchausti, P. (Eds.), Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford University Press: Oxford, p. 209-220.

Berg, M., De Ruiter, P., *et al.*, 2001. Community food web, decomposition and nitrogen mineralisation in a stratified Scots pine forest soil. Oikos 93, 130–142.

Berlow, E.L., Neutel, A.-M., *et al.*, 2004. Interaction strengths in food webs: issues and opportunities. J. Anim. Ecol. 73, 585–598.

Bloem, J., Breure, A.M., 2003. Microbial indicators. In: Markert, B.A., Breure, A.M., Zechmeister, H.G. (Eds.), Bioindicators and biomonitors. Trace Elements and other Contaminants in the Environment 6, 259-282. Elsevier: Amsterdam.

Bloem, J., Veninga, M., Shepherd, J., 1995a. Fully automatic determination of soil bacterium numbers, cell volumes and frequencies of dividing cells by confocal laser scanning microscopy and image analysis. Appl. Environ. Microbiol. 61, 926-936.

Bloem, J., Bolhuis, P.R., Veninga, M.R., Wieringa, J., 1995b. Microscopic methods for counting bacteria and fungi in soil. In: Alef, K., Nannipieri, P. (Eds.), Methods in Applied Soil Microbiology and Biochemistry. Academic Press: London, p. 162-173.

Bongers, T., 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83, 14-19.

Bongers, T., 1994. De nematoden van Nederland (2nd ed.). Natuurhistorische Bibliotheek 46.

Bongers, T., 1999. The Maturity Index, the evolution of nematode life history traits, adaptive radiation and *cp*-scaling. Plant Soil 212, 13-22.

Bongers, T., Van der Meulen, H., Korthals, G., 1997. Inverse relationship between the nematode maturity index and plant parasitic index under enriched nutrient conditions. Appl. Soil Ecol. 6, 195-199.

Bonkowski, M., 2004. Protozoa and plant growth: the microbial loop in soil revisited. New Phytol. 162, 617-631.

Botkin, D.B., 1990. Discordant Harmonies: A new Ecology for the Twentyfirst Century. University of California Press: Berkeley, CA.

Braun-Blanquet, J., 1951. Pflanzensoziologie. Grundzüge der Vegetationskunde (2nd rev. ed.). Springer Verlag: Wien.

Breure, A.M., 2004. Ecological soil monitoring and quality assessment. In: Doelman, P., Eijsackers, H.J.P. (Eds.), Vital Soil: Function, Value and Properties. Elsevier Science: Amsterdam. Developments in Soil Science 29, 281-305.

Breure, A.M., Mulder, Ch., *et al.*, 2003a. A biological indicator for soil quality. Proceedings OECD Expert Meeting on Soil Erosion and Soil Biodiversity Indicators, 25-28 March 2003, Rome, p. 485-494.

Breure, A.M., Rutgers, M., *et al.*, 2003b. Ecologische bodemkwaliteit. RIVM report 60760405, Bilthoven.

Breure, A.M., Mulder, Ch., Rutgers, M., Schouten, A.J., Van Wijnen, H.J., 2004. Belowground biodiversity as an indicator for sustainability of soil use. Grassland Science in Europe 9, 195-197. Arbeitsgemeinschaft zur Förderung des Futterbaues: Zürich.

Brose, U., Pavao-Zuckerman, M., *et al.*, 2005. Spatial aspects of food webs. In: De Ruiter, P.C., Wolters, V., Moore, J.C. (Eds.), Dynamic Food Webs: Multispecies Assemblages, Ecosystem Development, and Environmental Change. Academic Press [in press].

Brussaard, L., Bakker, J.P., Olff, H., 1996. Biodiversity of soil biota and plants in abandoned arable fields and grasslands under restoration management. Biodiv. Conserv. 5, 211-221.

Brussaard, L., Behan-Pelletier, V.M., *et al.*, 1997. Biodiversity and ecosystem functioning in soil. Ambio 26, 563-570.

Campbell, C.D., Chapman, S.J., Cameron, C.M., Davidson, M.S., Potts, J.M., 2003. A rapid microtiter plate method to measure carbon dioxide evolved from carbon substrate amendments so as to determine the physiological profiles of soil microbial communities by using whole soil. Appl. Environm. Microbiol. 69, 3593-3599.

Carpenter, S.R., 2000. Alternate states of ecosystems: evidence and its implications for environmental decisions. In: Press, M.C., Huntley, N., Levin, S. (Eds.), Ecology: Achievement and Challenge. Blackwell: London, p. 357-383.

Carpenter, S.R., 2002. Regime Shifts in Lake Ecosystems: Pattern and Variation. Excellence in Ecology Series 15. International Ecology Institute: Oldendorf/Luhe.

Carpenter, S.R., Walker, B.H., Anderies, J.M., Abel, N., 2001. From metaphor to measurement: resilience of what to what? Ecosystems 4, 765–781.

Chust, G., Pretus, J.L., Ducrot, D., Bedòs, A., Deharveng, L., 2003. Response of soil fauna to landscape heterogeneity: determining optimal scales for biodiversity modeling. Cons. Biol. 17, 1712-1723.

Cohen, J.E., Briand, F., 1984 Trophic links of community food webs. Proc. Natl. Acad. Sci. USA 81, 4105-4109.

Cohen, J.E., Carpenter, S.R. 2005. Species' average body mass and numerical abundance in a community food web: statistical questions in estimating the relationship. In: De Ruiter, P.C., Wolters, V., Moore, J.C. (Eds.), Dynamic Food Webs: Multispecies Assemblages, Ecosystem Development, and Environmental Change. Academic Press [in press].

Cohen, J.E., Newman, C.M., 1988. Dynamic basis of food web organization. Ecology 69, 1655-1664.

Cohen, J.E., Beaver R.A., *et al.*, 1993a. Improving food webs. Ecology 74, 252-258.

Cohen, J.E., Pimm, S.L., Yodzis, P., Saldaña, J., 1993b. Body sizes of animal predators and animal prey in food webs. J. Anim. Ecol. 62, 67-78.

Cohen, J.E., Jonsson, T., Carpenter, S.R., 2003. Ecological community description using the food web, species abundance, and body size. Proc. Natl. Acad. Sci. USA 100, 1781-1786.

Costanza, R., Cumberland, J., Daly, H., Goodland, R., Norgaard, R., 1997. An Introduction to Ecological Economics. CRC: Boca Raton, FL.

Cousins, S.H., 1980. A trophic continuum derived from plant structure, animal size and a detritus cascade. J. theor. Biol. 82, 607-618.

Cousins, S.H., 1985. The trophic continuum in marine ecosystems: Structure and equations for a predictive model. Can. Bull. Fish. Aquat. Sci. 213, 76-93.

Cousins, S.H., 1987a. The decline of the trophic level concept. Trends Ecol. Evol. 2, 312-316.

Cousins, S.H., 1987b. Can we count natural ecosystems? Brit. Ecol. Soc. Bull. 18, 156-158.

Cousins, S.H., 1996. Food webs: from the Lindeman paradigm to a taxonomic general theory of ecology. In: Polis, G.A., Winemiller, K.O. (Eds.), Food webs: Integration of Patterns and Dynamics. Chapman & Hall: New York, NY, p. 243-251.

Cross, E.A., Moser, J.C., 1975. A new dimorphic species of *Pyemotes* and a key to previously-described forms (Acarina: Tarsonemoidea). Ann. Entomol. Soc. Am. 68, 723-732.

Cross, E.A., Moser, J.C., Rack, G., 1981. Some new forms of *Pyemotes* (Acarina: Pyemotidae) from forest insects, with remarks on polymorphism. Int. J. Acarol. 7, 179-196.

Cyr, H., Downing, J.A., Peters, R.H., 1997. Density-body size relationships in local aquatic communities. Oikos 79, 333-346.

De Candolle, A., 1855. Géographie botanique raissonnée. Masson: Paris.

Dekker, S.C., Scheu, S., *et al.*, 2005. Towards a new generation of dynamical decomposer food web model. In: De Ruiter, P.C., Wolters, V., Moore, J.C. (Eds.), Dynamic Food Webs: Multispecies Assemblages, Ecosystem Development, and Environmental Change. Academic Press [in press].

De Ruiter, P.C., Van Veen, J.A., Moore, J.C., Brussaard, L., Hunt, H.W., 1993a. Calculation of nitrogen mineralisation in soil food webs. Plant Soil 157, 263-273.

De Ruiter, P.C., Moore, J.C., *et al.*, 1993b. Simulation of nitrogen mineralization in the below-ground food webs of two winter wheat fields. J. Appl. Ecol. 30, 95-106.

De Ruiter, P.C., Neutel, A.-M., Moore, J.C., 1994. Modelling food webs and nutrient cycling in agro-ecosystems. Trends Ecol. Evol. 9, 378-383.

De Ruiter, P.C., Neutel, A.-M., Moore, J.C., 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. Science 269, 1257-1260.

Díaz, A., Okabe, K., Eckenrode, C.J., Villani, M.G., O'Connor, B.M., 2000. Biology, ecology, and management of the bulb mites of the genus *Rhizoglyphus* (Acari: Acaridae). Exp. Appl. Acarol. 24, 85-113.

Duffy, J.E., 2002. Biodiversity and ecosystem function: the consumer connection. Oikos 99, 201-209.

Ekschmitt, K., Bakonyi, G., *et al.*, 1999. Effects of the nematofauna on microbial energy and matter transformation rates in European grassland soils. Plant Soil 212, 45-61.

Enkegaard, A., Sardar, M.A., Brødsgaard, H.F., 1997. The predatory mite *Hypoaspis miles*: biological and demographic characteristics on two prey species, the mushroom sciarid fly, *Lycoriella solani*, and the mould mite, *Tyrophagus putrescentiae*. Entomologia Experimentalis et Applicata 82, 135-146.

Ghilarov, M.S., 1944. Correlations between size and numbers of soil animals. C. r. Dokl. Acad. Sci. USSR 43, 267-269.

Ghilarov, M.S., 1965. Zoologische Methoden der Bodendiagnostik. Nauka: Moskow.

Heemsbergen, D.A., Berg, M.P., *et al.*, 2004. Biodiversity effects on soil processes explained by interspecific functional dissimilarity. Science 306, 1019-1020.

Hendriks, A.J., 1999. Allometric scaling of rate, age and density parameters in ecological models. Oikos 86, 293-310.

Hokka, V., Mikola, J., Vestberg, M., Setälä, H., 2004. Interactive effects of defoliation and an AM fungus on plants and soil organisms in experimental legume-grass communities. Oikos 106, 73-84.

Holling, C.S., 1973. Resilience and stability of ecological systems. Ann. Rev. Ecol. Syst. 4, 1-23.

Holling, C.S., 1986. The resilience of terrestrial ecosystems; local surprise and global change. In: Clark, W.C., Munn, R.E. (Eds.), Sustainable Development of the Biosphere. Cambridge University Press: Cambridge, p. 292-317.

Holling, C.S., 1992. Cross-scale morphology, geometry and dynamics of ecosystems. Ecol. Monogr. 62, 447-502.

Holling, C.S., Gunderson, L.H., Peterson, G.D., 2002. Sustainability and panarchies. In: Gunderson, L.H., Holling, C.S. (Eds.), Panarchy: Understanding Transformations in Human and Natural Systems. Island Press: Washington, DC, p. 63-102.

Hunt, H.W., Coleman, D.C., *et al.*, 1987. The detrital food web in a shortgrass prairie. Biol. Fertil. Soils 3, 57-68.

Ingham, R.E., Trofymow, J.A., Ingham, E.R., Coleman, D.C., 1985. Interactions of bacteria, fungi, and their nematode grazers: Effects on nutrient cycling and plant growth. Ecol. Monogr. 55, 119-140.

Jansa, J., Mozafar, A., *et al.*, 2002. Diversity and structure of AMF communities as affected by tillage in a temperate soil. Mycorrhiza 12, 225-234.

Kay, F.R., Sobhy, H.M., Whitford, W.G., 1999. Soil microarthropods as indicators of exposure to environmental stress in Chihuahuan desert Rangelands. Biol. Fertil. Soils 28, 121–128.

Kendall, H.W., Pimentel, D., 1994. Constraints on the expansion of the global food supply. Ambio 23, 198-216.

King, K.L., Hutchinson, K.J., Greenslade, P., 1976. The effects of sheep numbers on associations of Collembola in sown pastures. J. Appl. Ecol. 13, 731–739.

Krczal, H., 1957. Systematik und Ökologie der Pyemotiden. In: Stammer, H.-J. (Ed.), Systematik und Ökologie Mitteleuropäischer Acarina 1(1), 385-823. Akademische Verlagsgesellschaft: Leipzig.

Laakso, J., Setälä, H., Palojärvi, A., 2000. Influence of decomposer food web structure and nitrogen availability on plant growth. Plant Soil 225, 153-165.

Lancaster, J., 2000. The ridiculous notion of assessing ecological health and identifying the useful concepts underneath. Human Ecol. Risk Assessm. 6, 213-222.

Levin, S.A., 1999. Fragile Dominion: Complexity and the Commons. Perseus Books: Reading, MA.

Liiri, M., Setälä, H., Haimi, J., Pennanen, T., Fritze, H., 2002. Relationship between soil microarthropod species diversity and plant growth does not change when the system is disturbed. Oikos 96, 137-149.

Linné, C., 1784. *Systema vegetabilium secundum Classes Ordines Genera Species cum characteribus et differentiis*. Typis et impensis, Jo. Christ. Dieterich: Gottingae.

Markert, B.A., Breure, A.M., Zechmeister, H.G., 2003. Definitions, strategies and principles for bioindication/biomonitoring of the environment. In: Markert, B.A., Breure, A.M., Zechmeister, H.G. (Eds.), Bioindicators and biomonitors. Trace Elements and other Contaminants in the Environment 6, 3-39. Elsevier: Amsterdam.

Moore, J.C., Hunt, H.W., 1988. Resource compartmentation and the stability of real ecosystems. Science 261, 906-909.

Moore, J.C., Walter, D.E., Hunt, H.W., 1988. Arthropod regulation of micro- and mesobiota in below-ground detrital food web. Ann. Rev. Entomol. 33, 419-439.

Moore, J.C., Berlow, E.L., *et al.*, 2004. Detritus, trophic dynamics and biodiversity. Ecol. Lett. 7, 584-600.

Mulder, Ch., 1999. Biogeographic re-appraisal of the Chenopodiaceae of Mediterranean drylands: A quantitative outline of their general ecological significance in the Holocene. Palaeoecol. Afr. 26, 161-188.

Mulder, Ch., Ellis, R.P., 2000. Ecological significance of South-West African grass leaf phytoliths: A climatic response of vegetation biomes to modern aridification trends. In: Jacobs, S.W.L., Everett, J. (Eds.), Grasses. Systematics and Evolution 2, 246-256.

Mulder, Ch., De Zwart, D., 2003. Assessing fungal species sensitivity to environmental gradients by the Ellenberg indicator values of above-ground vegetation. Basic Appl. Ecol. 4, 557-568.

Mulder, Ch., Sakorafa, V., Burragato, F., Visscher, H., 2000. Ecohydrological perspective of phytogenic organic and inorganic components in Greek lignites: A quantitative reinterpretation. Earth Planet. Sci. Lett. 179, 167-181.

Mulder, Ch., Breure, A.M., Joosten, J.H.J., 2003a. Fungal functional diversity inferred along Ellenberg's abiotic gradients: Palynological evidence from different soil microbiota. Grana 42, 55-64.

Mulder, Ch., De Zwart, D., Van Wijnen, H.J., Schouten, A.J., Breure, A.M., 2003b. Observational and simulated evidence of ecological shifts within the soil nematode community of agroecosystems under conventional and organic farming. Funct. Ecol. 17, 516-525.

Mulder, Ch., Cohen, J.E., Setälä, H., Bloem, J., Breure, A.M., 2005. Bacterial traits, organism mass, and numerical abundance in the detrital soil food web of Dutch agricultural grasslands. Ecol. Lett. 8 [in press]. *Supp. Mat. available at:* http://www.blackwellpublishing.com/products/journals/suppmat/ELE/ELE704/ELE704sm.htm

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H., Woodfin, R.M., 1994. Declining biodiversity can alter the performance of ecosystems. Nature 368, 734-737.

Neutel, A.-M., Roerdink, J.C.T.B., De Ruiter, P.C., 1995. Global stability in detritus based food chains. J. theor. Biol. 171, 351-353.

Neutel, A.-M., Heesterbeek, J.A.P., De Ruiter, P.C., 2002. Stability in real food webs: weak links in long loops. Science 296, 1120-1123.

O'Connell, T., Bolger, T., 1997. Fungus fruiting bodies and the structure of fungus-micro-arthropod assemblages. Proc. Royal Irish Acad. 97B, 249-262.

Paine, R.T., 1980. Food webs: linkage, interaction strength and community infrastructure. J. Anim. Ecol. 49, 667-686.

Paul, E.A., Harris, D., Klug, M., Ruess, R., 1999. The determination of microbial biomass. In: Robertson, G.P., Coleman, D.C., Bledsoe, C.S., Sollins, P. (Eds.), Standard Soil Methods for Long-term Ecological Research. Oxford University Press: Oxford, p. 291-317.

PERISCOOP, 2003. Periscoop – platform ecologische risicobeoordeling (Van der Waarde J., Wagelmans, M., *et al*., Eds.). Eindrapport SP-015, Stichting Kennisoverdracht en Kennisontwikkeling Bodem, SKB: Gouda.

Peters, R.H., 1983. The Ecological Implication of Body Size. Cambridge University Press: Cambridge.

Petersen, H., 1981. The respiratory metabolism of Collembola species from a Danish beech wood. Oikos 37, 273-286.

Petersen, H., 1995. Energy flow and trophic relations in soil communities: State of knowledge two decades after the International Biological programme. In: Edwards, C.A., Abe, T., Striganova, B.R. (Eds.), Structure and Functions of Soil Communities, Kyoto University Press: Kyoto, p. 111-130.

Petersen, H., Luxton, M., 1982. A comparative analysis of soil fauna populations and their role in decomposition process. Oikos 39, 288-388.

Pimentel, D., Allen, J., *et al.*, 1987. World agriculture and soil erosion. BioScience 37, 277-283.

Radwan, J., Bogacz, I., 2000. Comparison of life-history traits of the two male morphs of the bulb mite, *Rhizoglyphus robini*. Exp. Appl. Acarol. 24, 115-121.

Reynoldson, T.B., Norris, R.H., Resh, V.H., Day, K.E., Rosenberg, D.M., 1997. The reference condition: a comparison of multimetric and multivariate approaches to assess water-quality impairment using benthic macroinvertebrates. J. North Amer. Benthol. Soc. 16, 833-852.

Rutgers, M., Faber, J., Postma, J., Eijsackers, H., 1998. Locatiespecifieke ecologische risico's: een basisbenadering voor functiegerichte beoordeling van bodem-verontreining. Rapporten Programma geïntegreerd Bodemonderzoek 16.

Sakai, A.K., Allendorf, F.W., *et al*., 2001. The population biology of invasive species. Annu. Rev. Ecol. Syst. 32, 305-332.

Salminen, J., Korkama, T., Strömmer, R., 2002. Interaction modification among decomposers impairs ecosystem processes in lead-polluted soil. Environ. Toxicol. Chem. 21, 2301-2309.

Scheffer, M., Carpenter, S.R., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413, 591-596.

Schönholzer, F., Hahn, D., Zeyer, J., 1999. Origins and fate of fungi and bacteria in the gut of Lumbricus terrestris L. studied by image analysis. FEMS Microbiol. Ecol. 28, 235-248.

Schouten, A.J., Van Esbroek, M.L.P., Alkemade, J.R.M., 1998. Dynamics and stratification of functional groups of nematodes in the organic layer of a Scots pine forest in relation to temperature and moisture. Biol. Fertil. Soils 26, 293-304.

Schouten, A.J., Rutgers, M., Breure, A.M., 2001. BoBI op weg – Tussentijdse evaluatie van het project Bodembiologische Indicator. RIVM report 607604002, Bilthoven.

Schouten, T., Breure, A.M., Mulder, Ch., Rutgers, M., 2004. Nematode diversity in Dutch soils, from Rio to a Biological Indicator for Soil Quality. Nematol. Monogr. Perspect. 2, 469-482.

Schröter, D., Wolters, V., De Ruiter, P.C., 2003. C and N mineralisation in the decomposer food webs of a European forest transect. Oikos 102, 294-308.

Setälä, H., Marshall, V.G.. Trofymow, T., 1996. Influence of body size of soil fauna on litter decomposition and uptake by poplar in a pot trial. Soil Biol. Biochem. 28, 1661–1675.

Setälä, H., Laakso, J., Mikola, J., Huhta, V., 1998. Functional diversity of decomposer organisms in relation to primary production. Appl. Soil Ecol. 9, 25-31.

Siepel, H., 1994. Life-history tactics of soil microarthropods. Biol. Fertil. Soils 18, 263-278.

Siepel, H., De Ruiter-Dijkman, E.M., 1993. Feeding guilds of oribatid mites based on carbohydrase enzyme activities. Soil Biol. Biochem. 25, 1491-1497.

Siepel, H., Maaskamp, F., 1994. Mites of different feeding guilds affect decomposition of organic matter. Soil Biol. Biochem. 26, 1389–1394.

Swift, M.J., Van der Meer, J., *et al*., 1996. Biodiversity and agroecosystem function. In: Mooney, H.A., Hall Cushman, J., Medina, E., Sala, O.E., Schulze, E.-D. (Eds.), Functional Roles of Biodiversity: a Global Perspective. John Wiley & Sons: Chichester, p. 261-298.

TCB (Technische Commissie Bodembescherming), 2000. Advies raamwerk voor ecologische inbreng op de beleidsterreinen bodembescherming, biodiversiteit en ruimtelijke ordening in relatie tot NMP-4 en de Vijfde nota Ruimtelijke Ordening. TCB A29(2000): Den Haag.

TCB (Technische Commissie Bodembescherming), 2003. Advies duurzaam bodemgebruik op ecologische grondslag. TCB A33(2003): Den Haag.

Tilman, D., 1996. Biodiversity: population versus ecosystem diversity. Ecology 77, 350-363.

Van de Leemkule, M.A., 2001. Characterizing land use related soil ecosystem health – discussion paper. Report R15, Technische Commissie Bodembescherming: Den Haag.

Van Genderen, H., Schoonhoven, L.M., Fuchs, A., 1997. Chemisch-ecologische flora van Nederland en België (2nd ed.). Natuurhistorische Bibliotheek 63.

Van Gestel, C.A.M., Koolhaas, J.E., 2004. Water-extractability, free ion activity, and pH explain cadmium sorption and toxicity to *Folsomia candida* (Collembola) in seven soil-pH combinations. Environ. Toxicol. Chem. 23, 1822-1833.

Van Veen, J.A., Paul, E.A., 1979. Conversion of biovolume measurements of soil organisms grown under various moisture tensions, to biomass and their nutrient content. Appl. Environ. Microbiol. 37, 686-692.

Von Liebig, J., 1840. Die Organische Chemie in ihre Anwendung auf Agricultur und Physiologie. Vieweg: Braunschweig.

Walker, B., Carpenter, S., *et al.*, 2002. Resilience management in social-ecological systems: a working hypothesis for a participatory approach. Cons. Ecol. 6, 14.

Wardle, D.A., 1995. Impacts of disturbance on detritus food webs in agro-ecosystems of contrasting tillage and weed management practices. Adv. Ecol. Res. 26, 105-185.

Wardle, D.A., 2002. Communities and Ecosystems. Linking the Aboveground and Belowground Components. Monographs in Population Biology 34.

Wardle, D.A., Bardgett, R.D., *et al.*, 2004. Ecological linkages between aboveground and belowground biota. Science 304, 1629-1633.

West, G.B., Brown, J.H., Enquist, B.J., 2004. Growth models based on first principles or phenomenology? Funct. Ecol. 18, 188-196.

Winemiller, K.O., 1990. Spatial temporal variation in tropical fish trophic networks. Ecol. Monogr. 60, 331-367.

Wolters, V., Silver, W.L., *et al.*, 2000. Effects of global changes on above- and belowground biodiversity in terrestrial ecosystems: Implications for ecosystem functioning. BioScience 50, 1089-1098.

Woodward, G., Ebenman B., *et al.*, 2005. Body-size determinants of the structure and dynamics of ecological networks. In: De Ruiter, P.C., Wolters, V., Moore, J.C. (Eds.), Dynamic Food Webs: Multispecies Assemblages, Ecosystem Development, and Environmental Change. Academic Press [in press].

Yeates, G.W., 1979. Soil nematodes in terrestrial ecosystems. J. Nematol. 11, 213-229.

Yeates, G.W., 2003. Nematodes as soil indicators: functional and biodiversity aspects. Biol. Fertil. Soils 37, 199-210.

Yeates, G.W., Bongers, T., 1999. Nematode diversity in agroecosystems. Agricult., Ecosyst. Environ. 74, 113-135.

Yeates, G.W., Bongers, T., De Goede, R.G.M., Freckman, D.W., Georgieva, S.S., 1993. Feeding habits in soil nematode families and genera – an outline for soil ecologists. J. Nematol. 25, 315-331.

Glossary

Accidentals, aliens and intruders – rare organisms, mostly relics of a precedent soil community, or invasive species.

Allometric relation – the scaling of the form and function of a given organism. Allometry is a central feature of biodiversity and dictates that nutrient cycling rates (pro capita) should decline with **body mass**.

Arbuscular mycorrhizal fungi (AMF) – this mycorrhizal type is a non-pathogenic endo-infection formed by Zygomycetes, whose hyphae penetrating the roots of plant-hosts produce finely branched arbuscules and vesicles. Therefore this plant-fungus association is currently called “vesicular-arbuscular” (VA or VAM). Symbiotic AMF-infections enhance the phosphorus supply to the plant-host. Thus, the **biogeography** of AMF-infected plants in temperate grasslands reflects P-supply. It differs from the other typical association between tree-roots and Basidiomycetes in boreal forests, in which the fungi form a shealth on the root’s surface extending outwards (*ectomycorrhizae*).

Arthropods (micro–, macro–) – any invertebrate animal with a segmented body, jointed limbs and external skeleton. According to their body size, arthropods are commonly classified as macro-arthropods (insects, spiders, isopods, centipedes) and micro-arthropods (**collembolans** and **mites**).

Assemblage – a dynamic community of organisms that have to co-exist somehow and compete with other species depending on their characteristics.

Autotrophs – organisms (green plants and some bacteria) able to form complex nutritional organic substances from simple inorganic substances as CO_2. Algae, mosses, ferns and higher plants form the base of the trophic pyramid. Higher plants provide also a habitat to other organisms. *SEE ALSO* **NET PRIMARY PRODUCTION**.

Biodiversity – refers to the extent of ecological, genetic and taxonomic diversity over all the spatial and temporal scales. S*EE* **FUNCTIONAL** *AND* **TAXONOMIC DIVERSITY**.

Biogeography – the study of geographical or altitudinal distributions of organisms.

Biomass – the product of **body mass** per **numerical abundance**. It provides the total weight in a given area or volume.

Body mass – determines the amount of resources individuals can exploit and their vulnerability to predation. Can be quantified as average or maximal weight. Decreasing averages of body mass with increasing farming pressure are known for **macro-arthropods**. An alternative measure for body mass is body size (length).

Bottom-up – any effect on a species or community originating from shifts at a lower **trophic level**, like soil nutrient accumulation leading to the partial replacement of above-ground plants.

Collembolans (Insecta: Apterygota) – small wingless arthropods with a body size of 1-8 mm in length. Most collembolans feed on organisms associated with the **rhizosphere**.

Connectedness web – a graphical form of **food-web** based on three variables: the number of species, the average **interaction strenght**, and the connectedness according to binary interacting elements (either C = 0, no interaction, or C = 1, interaction).

Detritus – any form of dead organic matter (plant debris including **litter** and decaying wood), dung, animal manure, as well as secreted and excreted products from living organisms (like root exudates).

Ecological amplitude – the maximal range of environmental condition within which a certain kind of organisms or taxa may occur.

Ecosystem – a biological community of interacting organisms within a particular habitat in a certain physical environment. *SEE* **MICROCOSM** *AND* **FOOD-WEB**.

Enchytraeids (Oligochaeta: Enchytraeidae) – pale-colored worms with a body size of 1 to 5 cm in lenght. They reach a high **numerical abundance** in acid soils with high organic matter content. They ingest plant remains and phytoliths (SiO_2), select fungal materials and consume droppings of **collembolans**. Enchytraeids may also ingest **nematodes**.

Endogeic or Endogé – unpigmented earthworms which continuously inhabit the organic-mineral horizons of the soil (e.g., *Aporrectodea caliginosa*). Feeding mostly on dead roots, these species are adapted for horizontal burrowing. In the field, endogeic earthworms exhibit increasing **numerical abundance** and **biomass** in response to labile organic carbon. With increasing temperatures, endogeics are favored. *SEE ALSO* **EPIGEIC**.

Energy channels – distinct bacterial and fungal energy pathways in **food-webs**. As bacteria and fungal-driven compartments are coupled at higher **trophic level** by generalists, these two channels are of great importance to the soil food-web stability.

Environment – the totality of the physical (abiotic) conditions affecting the metabolic processes of living organisms. *COMPARE WITH* **ECOSYSTEM.**

Epigeic or Épigé – pigmented earthworms occurring in plant debris such as wood, leaf litter, compost or manure (e.g., *Lumbricus rubellus*). Most of them are notably active in the decomposition process and affect therefore the carbon and nitrogen dynamics of decaying surface **litter**. These surface-dweller species are poorly adapted for burrowing. *SEE ALSO* **ENDOGEIC** *AND* **LUMBRICIDS**.

Feeding habits – the essential feeding types of **nematodes** (predator, omnivore, plant–, hyphal–, and bacterial–feeder) assigned according to their buccal cavities.

Food-web – a given set of organisms occurring in the **ecosystem**, together with **links** showing the kind of organisms that each kind of animals eats. If it incorporates **detritus** in the first trophic level, it is called detrital (soil) food-web.

Functional diversity – the actual extent of functional differences among all the species occurring in a community. Mostly inferred from the number of **functional groups**.

Functional groups – a set of organisms similar in their contribution to a specific process, activity or property of a given **ecosystem**. It may be difficult to assign organisms to a functional group at which species differences become significant.

Functional guild – single functional unit that incorporates any organism that acquires energy from a given source.

Functional web – a description or analysis of a food-web focused on the potential to process energy by prey and predators.

Generalized Linear Models (GLM) – this class of iterative weighted linear regressions allows the modelling of systematic effects by a suitable transformation, for instance by fitting on maximum likelihood estimation.

Habitat – a single community possessing uniformity with respect to a certain environmental quality. Habitats are separated by discontinuous properties in the physical environment.

Heterotrophs – organisms that have to derive their sustenance, enrichment and requirements from organic substances because they are unable to use CO_2 directly. *COMPARE WITH* **AUTOTROPHS**.

Humus – almost completely decomposed plant debris with no traces of the original morphology of the former material (leaves, wood, roots). According to the existence (or not) of an undecomposed top layer, it is further classified as mor (mull) humus. *SEE ALSO* **LITTER**.

Hysteresis – a different recovery trajectory of the **ecosystem** determined by management history and changes over time, corresponding to values of the unwanted property X at which $dX/dt = c - bX - \chi$ where c promotes X, and b represents the rate at which X decays in a system whose **resilience** is χ. *SEE ALSO* **STABLE STATES.**

Indifferent species – organisms without any definite affinity for a particular community.

Interaction strength – once a trophic **link** between two species has been established, the interaction strength has to be assigned from a specified distribution. Strong interactions (and an increased **connectedness**) are typical for a small community but are rare, as the most widespread interactions in nature are weak. Weaker interactions permit a much greater number of species to coexist in space. Therefore it is still "exceedingly difficult" to estimate the actual interaction strengths of species in space and time. Food-webs that include interaction strength in their algorithm show compartmentation.

Kurtosis – the sharpness of the peak of a frequency distribution or habitat-response curve of a certain kind of organism or species.

Life Support Function (LSF) – all the functions (*ecological services*) essential for both the environmental as the human health.

Link – a graphical simplification of a food chain (energy pathways). In more elaborated (sub)food-webs, their amount in space, time or compartment is named *link density*. *SEE ALSO* **INTERACTION STRENGTH.**

Litter – plant debris at various degrees of decomposition, in which the original morphology of the plant (leaves, wood, roots) are still visible. *SEE ALSO* **HUMUS**.

Livestock unit – the amount of cows, sheep, pigs and poultry excreting an average of 41 kg P_2O_5 (or 161 kg N) ha^{-1} yr^{-1}. One unit equals 1 cow, 8 calves or sheep, 5 pigs, etc.

Log-log regression – a linear regression fitted to data after applying a logarithmic transformation to both variables. The regression of y = log [individual **body mass**] should be written as a linear function of x = log [**numerical abundance** (per kg of soil)], that is, $y = \beta x + a$. Then the estimated slope 'β' is the quantity that in a stable **ecosystem** will be near -1. Which variable is taken as the independent variable (i.e., 'x') makes a great difference in the estimated slope. Our model was fitted using a $\log_{10}$-transformation, although a natural log-transformation would have given the same slope but a different intercept (other values on the axes). It does not matter if log is $\log_{10}$ or ln, as long as you use the same log for both variables.

Lumbricids (Oligochaeta: Lumbricidae) – burrowing "earthworms" consistently associated with mull **humus**. These worms play a key role in the mixture or organic matter with the mineral soil. According to their habitat and morphology, lumbricids are classified as **Epigeics**, Anecics or **Endogeics** (no burrowing, vertical burrows, and horizontal burrows). Lumbricids are used as indicators for soil structure and compaction.

Macroecology – the study of emergent statistical properties of large sets of ecological data (depicting **assemblages** of species distributed over space and time) to find general patterns at scales not amenable to standard deductive methods. Derived patterns are used to develop new hypotheses for constraining processes.

Microcosm – a miniature experimental representation of a given environment under standardized conditions for developing ecological theory.

Microflora – Bacteria, Fungi and yeasts.

Mites (Acarina: Astigmata, Mesostigmata, Prostigmata and Oribatida) – small arachnid arthropods with simple eyes and four pairs of legs when adult. Body sizes may range in length from 150 µm to over 2 mm. Mites to be found in the **litter** belong to diverse **functional guilds** according to their mode of feeding, although the typical arachnid mode of feeding is predation.

Nematodes (Nematoda) – pale-colored elongated roundworms with a body size of 500 µm to over 1 cm in length and different **feeding habits**. Under certain environmental conditions, some bacterivore nematodes enter a diapause. During this resting stage, ended by an appropriate environmental stimulus, they are named *dauerlarvae*.

Net Primary Production (NPP) – the amount of green plant tissues formed through photosynthesis by different plant species and accumulated within a given area (from square meters up to hectares, depending on the vegetation type) over a given period of time (mostly a year).

Niche – a position or role within a community taken by a species, or a region where a species occurs. Within its discrete boundaries, that species is expected to grow with vigor. *SEE ALSO* **BIOGEOGRAPHY**.

Numerical abundance or density – the number of organisms of a certain kind per given unit (volume, area or weight). As numerical abundance is a population level parameter, the abundance response is the final level of response of an environment.

Phytophagous – any organisms ingesting plant tissues, thus feeding on **primary producers**. Detrital macrophytopages feed on roots, rhizomes, and bulbs of plants. Microphytophages feed on fungi, bacteria and yeasts. One organism feeding on both **microflora** and **detritus** is usually called panphytophagous (mainly **arthropods**).

Preferential species – organisms whose **numerical abundance** strongly fluctuates although they show a greater deal of vigor in a given management regime and/or in a certain type of soil

Prey preference – we have chosen for the assumption that every kind of predator has a constant, independent probability of feeding on every kind of prey in a given **food-web**. If this parameter is not kept constant, the resulting model predicts the prey preference for a given species in that food-web. When a predator shares a common resource with its prey, an intraguild predation occurs.

Primary decomposers – bacteria and fungi (primary consumers **trophic level**).

Primary producers – **autotrophs** (algae, macrophytes, trees, etc.).

Proxy – an integrated attribute gathered from field records and laboratory data.

Randomized block design – an experimental design that reduces the probability of false segregation of treatments in the field.

Redundancy – a measure of the extent to which species occurring within a given **functional group** or **ecosystem** are (partially) substitutable.

Resilience – the speed at which a given **ecosystem** returns to its original state after a disturbance and the degree to which the **ecosystem** is capable of self-organization.

Resistance – the extent to which a given **ecosystem** keeps its original state during an external disturbance. In the case of an unstable **ecosystem**, this measure of ability can be seen through time as *persistence*.

Rhizosphere – the interface between living plant tissues (roots, bulbs etc.) and dead organic matter. *SEE ALSO* **DETRITUS**.

Selective species – organisms found frequently in a certain community, although they are not completely confined to one community as the exclusive species.

Soil respiration – basal microbial activity, where the CO_2 evolution under standardized conditions is measured without substrate addition after 2-6 weeks of incubation in the laboratory.

Stable states – states of one **ecosystem** that do not change over time, corresponding to values of X at which $dX/dt = \alpha - \chi = 0$ if any disturbance $h(\alpha)$ exceeding the ecosystem's **resilience** χ is absent (thus, $\chi \leq \alpha$). Any environmental disturbance can be split in two components according to $h(\alpha) = -bX + c$ where b represents the rate at which the unwanted property X decays in the ecosystem and c promotes X. The dynamics between b and c (the two opposite components of any disturbance) may cause significant recovery delay over time (**hysteresis**) of the original state.

Studentized residuals – a non-parametric locally-weighted-scatterplot smoother that uses data from a neighborhood around one specific abiotic predictor-value, supposing to reveal the underlying pattern without any preconception of what that relationship is. The removal from the data set of exceptional values and outliers (here identified by their Studentized residual if $> |2|$) makes such estimates more robust.

Succession – the result of natural or forced developmental changes. Any **ecosystem** (e.g., soil system) or community (e.g., vegetation unit) experiences successional processes. These processes can be regarded as *primary* (on bare ground in absence of previous species) or *secondary* (degradation after disturbance). The whole succession is a continuous process that involves the migration of species together with changes in **numerical abundance**.

Sustainability – one dynamic equilibrium allowing the survival and/or persistence of a certain **ecosystem**. A sustainable system means avoiding extinction and hedging against instabilities and dysfunctions.

Taxa (plural of **Taxon**) – any taxonomic group. In this report we use this term as soon the level of classification (**taxonomical resolution**) for the organisms occurring in a given sample differs (for instance, genera and families for **nematodes**, but species for **lumbricids** or **micro-arthropods**).

Taxonomic diversity – the absolute number of **taxa** occurring in the investigated area. In the case of bacterial community, it can only be derived from the amount of DNA banding patterns.

Taxonomical resolution – the resolving power of classifying (soil) organisms. Some organisms can be easily recognized at species level, other only at order level.

Top-down – any effect on a species or community originating from shifts at a (much) higher **trophic level**. **Net primary productivity** and above-ground pressure are supposed to have interactive effects on the soil **taxonomic diversity**, although there is increasing evidence that this kind of **trophic cascade** is rare (or even absent) in detrital **food-webs**. *COMPARE WITH* **BOTTOM-UP**.

Trophic cascades – mostly predator effects across a structured **food-web**. Frequent in a system where the prey, with a **body mass** that is orders of magnitude smaller than that of their predators, cannot achieve a stable condition. Cascades in time are a key issue due to predation and resource limitation. *SEE ALSO* **BOTTOM-UP** *AND* **TOP-DOWN**.

Trophic level – trophic groups in a **food-web**, defined in our case as follows: **detritus** (1st trophic level) and its **primary decomposers** (2nd trophic level), detritivores (2nd trophic level), their predators (3rd trophic level) and top predators (4th trophic level and higher). *SEE* **PRIMARY PRODUCERS.**