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Sebastián I. Muñoz
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PREFACE

The new book presents important recent research on ecology which is the study of the interrelationships between organisms and their environment, including the biotic and abiotic components. There are at least six kinds of ecology: ecosystem, physiological, behavioral, population, and community. specific topics include: Acid Deposition, Acid Rain Revisited, Biodiversity, Biocomplexity, Carbon Sequestration in Soils, Coral Reefs, Ecosystem Services, , Environmental Justice, Fire Ecology , Floods, Global Climate Change, Hypoxia, and Invasion.

Chapter 1 - The ecological sciences provide a wealth of scientific information useful for setting policy and establishing management practice. The abundance of publications produced by ecologists contain various explanations of observed phenomena, identification of problems (often global), and descriptions of relationships and patterns in various biotic systems. It is this latter discipline, especially the descriptions of patterns in ecological relationships, that provides realistic guidance for decision-making. The other aspects of ecological science, while not directly useful in management, are relevant, in part because they contribute to our understanding of how patterns serve to guide management – management wherein the subjects of study of these other components of the ecological sciences are themselves taken into account. Patterns are defined herein as sets of information that by abundance and repetition identify limits to natural variation thereby differentiating normal and from pathological. Such patterns are exemplified by macroecological patterns. Normal cases exemplify sustainability compared to cases that are abnormal or pathological and unsustainable under the same circumstances. For example, patterns in predator-prey relationships among non-human species can be used to establish sustainable levels of resource use by humans; patterns in selectivity by non-human species can be used to implement evolutionarily enlightened management through selectivity by humans that mimics the selectivity of non-human species.

This chapter illustrates the use of patterns to establish sustainable harvests (consumption) from ecosystems, from individual species, and from groups of species. Other patterns illustrate sustainable allocations of harvests among alternative species. Still others illustrate the advisable size for protected areas along with their optimal locations. The authors chapter specifies the best science for management (and specifically for ecosystem-based fisheries management): the science that characterizes patterns that are integrative of complexity through the processes and factors that contribute to their origin – their emergence. More precisely, this science provides characterization of patterns that are consonant or isomorphic with the specific management questions being addressed. This is in contrast to the current use of scientific information. In conventional management, the ecological information we choose for determining management policy demands, and relies on, non-objective opinion and mistranslation of piecemeal information – often as patterns, but rarely consonant with management questions. The human conversion of non-consonant information to consonant information of conventional management is to be contrasted with the consonance of patterns that require no conversion in systemic management. In this way, systemic management, as pattern-based management, is objective, consistent, and widely, if not universally, applicable.

Chapter 2 - Understanding how abiotic factors regulate soil microbial activity is key in understanding the responses of terrestrial ecosystems to anticipated climate change. Soil microbes catalyze biogeochemical reactions and the exchange of nutrients between heterotroph and autotroph organisms, as well as between the soil and atmosphere. Semiarid forests are driven by "pulses" of precipitation (episodic and irregular events of precipitation) which activate soil microbial activity and their processes. Our knowledge on the functioning of semiarid forest ecosystems in response to pulse events has increased substantially over the last decade. However, a comprehensive paper synthesizing this literature and making conceptual progress at global scale is yet missing. This paper is a review of the current knowledge on microbial populations and their processes in forest semiarid ecosystems after pulse events. First, the authors briefly describe distribution and abundance of soil microbial biota in these systems. Second, the authors review ecosystem processes, and how they are regulated by microbial communities. These ecosystem processes include soil respiration, carbon and nitrogen dynamics and decomposition. Third, the authors address the effects that climatic change may exert on these populations and processes. The effects described are increased CO2 concentrations, elevated temperatures and changes in precipitation regimes.

Chapter 3 - The emissions of NO_x and NH_3 into the atmosphere are on the rise, and the emitted N compounds are distributed globally, causing concerns over possible effects on human health and the environment. The emission of N occurs primarily from agricultural activities and fossil-fuel combustion (e.g., automobile and industrial boilers). Atmospheric N deposition has become an important factor affecting forest health and sustainability in recent decades, partly as a result of decreasing S emissions. Nitrogen compounds that fall onto soil and water bodies with precipitation and dry deposition can cause damage to ecological systems. Chronic excessive N input can lead to base cation depletion, nutrient imbalances, eutrophication, soil acidification, and forest dieback. Leaching losses of NO_3^- gradually decrease the acid buffering capacity of forest soils. Moreover, releases of Al and Mn induced by soil acidification cause toxicity to trees. Biological processes play a crucial role in soil acidification, as N compounds originated from atmospheric deposition undergo nutrient cycling processes. However, the effects of N transformation on soil acidification in forest ecosystems are often overlooked. Thus, an improved understanding of the impact of atmospheric N deposition on N cycling processes is needed to better predict the responses of forest ecosystems to such depositions. In this paper, the authors explore the linkage between N cycling and soil acidification in forest ecosystems, and evaluate the role of N cycling and atmospheric N deposition on soil acidification in forest ecosystems by discussing: 1) the N cycle and its effect on soil acidification in forest ecosystems, 2) the effect of N deposition on forest soils and trees, in terms of base cation depletion, soil acidification, and aluminum toxicity, 3) leaching losses of N from forest soils, and 4) critical loads of atmospheric N deposition in forest ecosystems.

Chapter 4 - Many orders and families of invertebrates have been promoted as ecological and environmental indicators of management practices and natural disturbances in forest ecosystems. To date most research has focused on ants, particularly for gauging the success of efforts to restore lands modified by human disturbance. However, it is now recognised that a range of taxa are potentially required. Here, beetles, butterflies, ants and spiders have received interest as potential candidates for the 'shopping basket'. Less well known, but of great importance, are responses by the hyperdiverse order Hemiptera (true bugs). Recent research along a latitudinal gradient shows Hemiptera to be one of the best orders of invertebrate at discriminating between different forest types. This paper reviews the benefits of incorporating Hemiptera into ecological studies examining forest management practices. The authors describe the contribution Hemiptera make as the fifth most speciose insect order to forest biodiversity, their functional role in ecosystems, and their role as forest pests. Hemiptera occur in all forest strata (e.g., soil, leaf-litter, understorey, overstorey). As abundant and diverse prey they are likely to contribute to the high diversity of other arthropods plus insectivorous birds, mammals and reptiles. Although most Hemiptera are herbivorous, the group exhibits a wide spectrum of feeding habits, including predators, fungivores, and parasites. Even within the herbivores there is great variation owing to different host specificity levels, with some species highly monophagous (feeding only from one species of plant), through to species that are highly polyphagous (feeding from different families of plants). As many polyphagous Hemiptera often target plants with high nutrients, individual plants within a species may also differ in their hemipteran assemblages owing to differences in nutrients. This diversity in trophic requirements means that Hemiptera are sensitive to changes not only in habitat structure, but also floristics and changes in plant chemistry. Similarly, seasonal changes can also influence the structure of hemipteran assemblages at spatial scales ranging from individual plants up to forest plots. The authors review the most efficient methods for sampling Hemiptera, for example, beating, pitfall traps, vacuum sampling, intercept traps and chemical knockdown. The authors examine current knowledge on the response and recovery of Hemiptera to different forest disturbances, such as fire, fragmentation, windthrow, disease and flood. The authors then illustrate these points by summarizing studies in a forest system being restored following the severe disturbance of mining. Finally, the authors detail the role that both introduced and native species of Hemiptera display as pests in forest or silvicultural systems, as outbreaks of Hemiptera can indicate when a system is stressed, particularly by drought or flooding.

Chapter 5 - The main objective of the present study was to determine the effect of the type of pedogenesis generated by two different parent materials – amphibolite (AMP) and granite (GR) - and the effect of different forest stands - pine (P), eucalypt (E), and oak (O) – on the quality and quantity of organic C pools in udic, mesic and freely drained systems. Five C pools were studied: aboveground biomass, belowground biomass, dead wood, litter, and soil organic matter (SOM) in the Ah horizons. The three forest soils derived from AMP materials (AMP-P, AMP-E, AMP-O) were classified as Typic Fulvudands and Aluandic Andosols, and the three forest soils derived from GR rocks (GR-P, GR-E, GR-O) were classified as Humic Dystrudepts, and Leptic and Haplic Umbrisols. All soils are located in the surroundings of Santiago de Compostela (A Coruña, NW Spain), where the mean annual air temperature is 12.3 ºC and the total annual precipitation is 1624 mm yr^{-1}. The results obtained indicate that highest total organic C stocks in the ecosystems studied (down to the lowest depth of the Ah horizons), i.e., the sum of the five reservoirs considered, always corresponded to the eucalypt stands, with stocks > 500 t ha^{-1}, whereas those of the oak and pine stands were always < 500 t ha^{-1}. The mean distribution of organic C stocks in the five reservoirs considered was as follows: aboveground biomass, 18.4%; belowground biomass 4.6%; dead wood, 1.1%; litter 8.4%; and soil organic C, 67.2%; there were no significant differences ($P < 0.05\%$) between means of the AMP and GR ecosystems although the total C stocks were always higher in the AMP than in the GR ecosystems, and followed the order E > P > O in both. There were significant differences ($P<0.05$) in the quantity, quality and dynamics of organic C in the two types of ecosystems, when organic layers (L and F) and also Ah horizons (Ah1 and Ah2) were distinguished, as discussed below.

The results indicate that, in soils developed from GR, the lithology mainly determines the type of pedogenesis taking place in the surface horizons, with intense acidification (acid-complexolysis) associated with scarce or nil neoformation of secondary minerals in the most acidic compartments (L and F layers) and an abundance of aqueous and mobile organo-metal complexes. Under such conditions, decomposition of primary OM is very slow, leading to the accumulation of undecomposed debris in the organic layers. In soils developed from AMP, both lithology and plant species clearly affected pedogenesis in the surface horizons. Surface acidification occurred in the pine stand (although never as intense as that occurring on GR materials), but greater than that of AMP-E and AMP-O litters. In general, the more eutrophic conditions of the AMP soils, compared with the GR soils, appeared to allow rapid decomposition of primary OM. The geochemical conditions of the AMP Ah horizons also appeared to allow neoformation of metastable forms of gibbsite and different short-range order 1:1 aluminosilicates able to bind to secondary organic compounds. Under such conditions, decomposition of secondary OM was probably preserved, as reflected by the high organic C content of the Ah horizons. All of this may explain the existence of a moder-type OM in the GR soils, in comparison with the Al-mull type form of the AMP soils. Overall, the results obtained indicate that parent material affects the distribution within the soil profiles studied, as well as on its quality and dynamics within the soil profiles studied, whereas the organic C stocks present in the aboveground biomass were more affected by the type of forest species and management.

Chapter 6 - That humans evolved as a result of a move from forests to more open plains is still the prevailing paradigm in anthropology, and researchers often assume that this transition influenced the origins of human bipedalism, omnivory, tool use, large brains, and even speech. Here, the authors argue that there are no scientific grounds on which to base such a hypothesis. While we agree that *Homo* may have evolved in more open (tree-poor) habitats than other apes (which could account for our relatively poor climbing skills), the suggestion that humans shifted to drier habitats away from water is, according to our research, unproven. The authors propose instead a more parsimonious model compatible with all known data and corroborated by a number of independent sources of evidence.

Comparisons of the locomotor styles and nutritional requirements of extant species and anatomical comparisons of fossil and extant species including *Homo sapiens*, especially in combination with palaeoecological data, strongly suggest that early *Homo* evolved at the water's edge (whether in savannahs or elsewhere) where resources essential for brain growth were both abundant and easily procurable by a thick-enameled tool-using omnivorous hominid.

Chapter 7 - Ecosystem engineers function as regulators of ecosystem functions by influencing the fluxes of energy and materials across different spatial and temporal scales.

Understanding how ecosystem engineers affect the dynamic of heterogeneity in ecosystems is becoming a fundamental component of both theoretical and applied Ecology. This manuscript offers a conceptual discussion for characterizing how and why soil engineers (earthworms, termites and ants) affect heterogeneity patterns.

There are two types of ecosystem engineers in soils. Extended phenotype engineers concentrate their activities on the building of biogenic structures (earthworm casts, galleries and nest structures) in order to maintain optimal conditions for their growth. Conversely, accidental engineers expend energy in moving through the soil to find their optimal environment. Although both types of engineers create patches in an ecosystem, the authors argue that extended phenotype engineers have more effects on ecosystem heterogeneity since their activities are more concentrated in space, as compared to accidental engineers, which move and contribute to homogenisation of ecological processes throughout the whole ecosystem. Finally, the authors discuss how soil engineers affect ecosystem processes (e.g., carbon, water, and nutrient cycling) at higher scales than those of their own functional domains. While some biogenic structures can be looked on as patches or hot-spots without any interactions with their neighbourhoods at small space scales, others interact and constitute gradients and networks that significantly affect ecosystem processes, such as the population dynamic of trees or soil erosion at the landscape scale.

The authors argue that it is necessary to have a quantitative knowledge on the size, boundaries and dynamics of patches created by soil engineers. Embracing the links between the ecology of engineers and the frontiers of their sphere of influence will enhance understanding how spatial heterogeneity regulated by ecosystem engineers affect pools and fluxes in ecosystems.

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Expert Commentary

NEW DIRECTIONS IN PALAEOANTHROPOLOGY

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Anthropology, a specific subfield of ethology, because it deals specifically with our own species, tends to be characterized by a more emotional approach than is common in other ethological fields. This may explain why standard methods that are commonly used in ethology, such as comparative biology, are remarkably rare in anthropology and especially palaeoanthropology. Anthropologists tend to view humans as unique, and therefore fail to apply comparative methods on humans and their fossil and living relatives, as would be done as a matter of practice in a number of other fields. As long as this anthropocentric attitude continues, it will remain impossible to reconstruct human evolution in an objective manner.

It is now more than half a century ago that Max Westenhöfer (1942), and later Sir Alister Hardy (1960), proposed on the basis of comparisons with other animals that humans were more aquatic than had generally been accepted. They had noticed (independently) that humans differ from other primates by possessing a much thicker layer of fat directly under the skin, and by lacking fur on most parts of their body. To them, this was a striking similarity to other furless mammals with high amounts of subcutaneous fat. All mammals that are both fat and naked are either fully aquatic or tropical semi-aquatic (the reverse does not necessarily hold), for instance, the Sirenia, Cetancodonta (whales, dolphins and hippopotami) and some Suidae and Pinnipedia. Since this is the case, why should humans be an exception? When Hardy (1960) straightforwardly suggested that this might point to a semi-aquatic past for our ancestors in tropical regions, he was either ignored or ridiculed by nearly all anthropologists. It was then believed (for reasons we describe in Chapter 6, “The original econiche of the genus *Homo*: open plain or waterside?”) that humans had evolved directly from forest dwellers (quadrupedal non-human primates) to become open plain dwellers (bipedal

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humans). The fact that other primates that went from forests to open plains, such as savannah baboons, had not lost their fur, had not developed large subcutaneous fat tissues, and had in fact become more quadrupedal rather than bipedal, was and still is apparently of no concern for those favouring the 'quadrupedal = forest, bipedal = open plain' model.

Whenever fossils of possible human relatives are found, the palaeofauna and -flora tend to be viewed in light of the open plain interpretations, and most interest therefore focuses on whether the landscape was open or forested. The fact that aquatic taxa are prevalent at many sites (see Chapter 6) seems inconsequential, and these are usually only referred to in scientific papers if they add something to the dating, stratigraphy or taphonomy. This unbalanced focus can be explained by the implicit or explicit conviction that the open plain or savannah view of human evolution is beyond doubt, an attitude which we think is largely due to a combination of educational biases and anthropocentrism. It is difficult to understand, for example, that anthropologists rarely consider the obvious fact that what is true for other animals (for instance, "all fat and naked mammals spend a lot of time in the water") might also be true for human ancestors.

It is clear to us that a reconsideration of the usual anthropological models for human evolution without anthropocentric biases will open new insights into how our ancestors evolved. In Chapter 6, we first reconsider the 'open plain' idea by examining one of its most recent incarnations, the 'endurance running' model, and show by using objective criteria such as comparative data that there is no support for a savannah or endurance running based interpretation of our past evolution. We then reconsider the sites of fossil *Homo* in an unbiased way, and conclude that most if not all sites were clearly at the waterside.

In our opinion, the reconstruction of the evolutionary history of a living species should be based in the first place on behavioural, anatomical and physiological comparisons of the species to its extant relatives and to other animal species, rather than on the interpretation of fossil finds. This is primarily because making sense of the (usually patchy, incomplete and scanty) fossil record strongly relies on interpretations, and it is never certain whether the supposed ancestor was an evolutionary dead end or really was an ancestor of a living species: we know we had ancestors, but we do not know whether fossils have descendants. At the same time we think that anthropologists need to acknowledge how unlikely it is that human subcutaneous fat, furlessness, breath-hold capacities and poor olfaction could have evolved because human ancestors lived in dry, open habitats.

We suggest two methods should be employed more frequently for future research into reconstructions of how human ancestors may have lived:

(1) In describing the accompanying palaeoflora and -fauna of a hominid site, attention is often given to the larger mammals and to the animals that can be thought to elucidate the supposedly savannah lifestyle of our ancestors. We suggest that the invertebrate, fish, avian, reptilian and smaller mammal fauna should also be studied in detail, and that anthropologists should keep an open mind to the possibility that not only the savannah itself, but the waterside, whether in the savannah or not, might be an essential element in human and hominid evolution. It is true that fossilisation in terrestrial settings mostly occurs in sedimentation in quiet waters and that this alone by no means suggests that the animals fossilised lived in these waters, but it is also the case that this does not exclude the possibility that they might have spent more or less time in these waters. Preliminary (Verhaegen and Puech 2000) and more

thorough studies (Munro 2004, and Chapter 6 in this book) of the fauna associated with hominid palaeoenvironments reveal that the aquatic components are often both significant and considerable.

(2) Anthropologists who construct models of the original human econiche tend to focus on the fossil evidence. But while the fossil record can provide crucial insights, its importance can also be overstated. Fossils are incomplete, typically they are fragmented pieces of bone without soft parts, and their exact phylogenetic relationship to living species is often uncertain. Frequently, species, age and sex are unknown, and the geological age and palaeoenvironment uncertain. The comparative method, which compares the behaviour, anatomy, physiology and DNA of *living* animals, is more secure, systematic and reliable than the fossil evidence. Therefore, we think thorough inventories and comparisons of the most diverse features of the most diverse animals are needed in order to discover correlations between these features.

Human features such as language and bipedal locomotion are often seen as unique, and consequently anthropologists tend to rely on functional interpretations instead of comparative arguments. But functional interpretations often mean subjective ‘explanations’: since we ‘know’ our ancestors lived on the savannah, it is easy to conclude that in humans, unlike savannah mammals, the function of subcutaneous fat, for example, was for thermal insulation in the cool savannah night, or as an energy depot to combat extended dry seasons. And because it is ‘known’ human ancestors were living on the savannah, there is no need to consider that subcutaneous fat, seen in all fully aquatic and many part-time water dwelling mammals but never in typical savannah mammals, could have been an adaptation to part-time water dwelling (be it for energy storage, thermo-insulation, streamlining, buoyancy or some other reason).

That some human features can appear to be unique, such as our language and locomotion, does not mean that comparisons with other animals can not be made. What is required is to separate these features into as many individual components as possible (ideally these components should be independent from each other). The finer the distinctions, the more detailed reconstructions can be obtained. Since biological features are generally inherited independently of each other (Mendel’s Laws), due to the crossing-over and re-assortment of chromosomes during meiosis, there is no reason not to use an analytic approach.

We provide a possible illustration as a starting-point for future research. It is often believed that human locomotion was an adaptation to the open plains, but when we separate our locomotion into its individual elements, this belief appears to be a just-so interpretation:

a) *two-leggedness* is seen in birds (including ostriches, flamingoes and penguins), many dinosaurs, and diverse mammals (including hopping mice and kangaroos on the savannah, indris and gibbons in the branches, and lowland gorillas and proboscis monkeys while wading, though not in most wading mammals);

b) *full plantigrady* (with the heels usually touching the ground or branch) is, for instance, seen in water opossums and sealions, whereas cursorial animals run on their toes or hooves (digiti- or unguligrady);

c) *very long legs* relative to trunk length are typical of frogs, kangaroos, indris, tarsiers, giraffes, ostriches and flamingoes, to name a few;

- d) *straight legs* (as opposed to bent-knees-bent-hips in rest) are seen from wading-birds to giraffes, especially in large and heavily-built species;
- e) *a striding gait* (with alternating limbs, as opposed to hopping) is seen in many walking, running and wading birds, and more frequently in larger-sized than in smaller birds;
- f) *truncal erectness* is seen in some arboreal species (especially tarsiers and gibbons), meerkats on the look-out, penguins on land, etc.;
- g) *a latero-laterally broad trunk* is typically seen in beavers and platypuses, and to a lesser degree in brachiating primates (apes and atelids);
- h) *an alined body* (with head, trunk and legs in one line) is typical of swimming animals; and so on.

While we realise that these resemblances are often subjective and that the comparisons are preliminary, they nevertheless indicate that humans resemble cursorials (c) less than they resemble arboreals (c, f), waders (c, d, e) and swimmers (b, g, h). This would be consistent with an idea that human ancestors were once tree dwellers who learnt to wade, swim and run.

This exercise can be repeated with all other features in which humans differ from our closest relatives the chimpanzees: furlessness, subcutaneous fat, olfactory reduction, external nose, parabolic tooth row, very large brain, and even human speech can be analysed into smaller elements (Verhaegen and Munro 2004). By combining all these results, we can develop a data set that can be used to evaluate various models of human evolution, including the ‘waterside’ and ‘open plain’ models.

In our opinion there has been too much focus on the role of open plains in human evolution, and not enough consideration given to the role of waterside habitats. Decisions of which data to collect and which models to test are compromised because of a widespread acceptance within the anthropological community that human evolution took place on the savannah. To redress this imbalance and to ensure a more objective approach, we believe that the study of how human ancestors lived will be greatly improved by (1) a non-savannah focused reconsideration of the fossil palaeoenvironment, and even more so by (2) a detailed and analytical comparison of typical human features with the widest possible range of animals.

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Chapter 1

ECOLOGY FOR MANAGEMENT: PATTERN-BASED POLICY

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ABSTRACT

The ecological sciences provide a wealth of scientific information useful for setting policy and establishing management practice. The abundance of publications produced by ecologists contain various explanations of observed phenomena, identification of problems (often global), and descriptions of relationships and patterns in various biotic systems. It is this latter discipline, especially the descriptions of patterns in ecological relationships, that provides realistic guidance for decision-making. The other aspects of ecological science, while not directly useful in management, are relevant, in part because they contribute to our understanding of how patterns serve to guide management – management wherein the subjects of study of these other components of the ecological sciences are themselves taken into account. Patterns are defined herein as sets of information that by abundance and repetition identify limits to natural variation thereby differentiating normal and from pathological. Such patterns are exemplified by macroecological patterns. Normal cases exemplify sustainability compared to cases that are abnormal or pathological and unsustainable under the same circumstances. For example, patterns in predator-prey relationships among non-human species can be used to establish sustainable levels of resource use by humans; patterns in selectivity by non-

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human species can be used to implement evolutionarily enlightened management through selectivity by humans that mimics the selectivity of non-human species.

This chapter illustrates the use of patterns to establish sustainable harvests (consumption) from ecosystems, from individual species, and from groups of species. Other patterns illustrate sustainable allocations of harvests among alternative species. Still others illustrate the advisable size for protected areas along with their optimal locations. Our chapter specifies the best science for management (and specifically for ecosystem-based fisheries management): the science that characterizes patterns that are integrative of complexity through the processes and factors that contribute to their origin – their emergence. More precisely, this science provides characterization of patterns that are consonant or isomorphic with the specific management questions being addressed. This is in contrast to the current use of scientific information. In conventional management, the ecological information we choose for determining management policy demands, and relies on, non-objective opinion and mistranslation of piecemeal information – often as patterns, but rarely consonant with management questions. The human conversion of non-consonant information to consonant information of conventional management is to be contrasted with the consonance of patterns that require no conversion in systemic management. In this way, systemic management, as pattern-based management, is objective, consistent, and widely, if not universally, applicable.

INTRODUCTION

Ecological research has resulted in a vast array of published information. New journals, books, and papers are published at a rate impossible for anyone to absorb completely. Today's ecologists cannot keep pace with the new work in their field, cannot claim to understand all of what has been published in the past, and cannot absorb work accomplished in other fields of science. Managers face an even more daunting task with the demands made by stakeholders. It is impossible to take all the information produced and combine it so as to objectively provide management advice. In current practice, the sheer volume of information before us contributes to our inability to translate scientific information to useful management advice. The overall impossibility of the current method of translation has been referred to as the 'Humpty-Dumpty phenomena" (Fowler 2003). This impasse is expressed in three ways. First, there is too much information to realistically assimilate or synthesize with the techniques used in today's management. Second, each piece of information is a reductionistic part that is subject to dualism; such items of information are understood only partially in their original context. Third, the parts we have to work with are conceptual and not the reality to which the concepts pertain. Not only are there too many parts to combine realistically, but also, we lack sufficient understanding to see how the parts fit together again. The whole is more than the sum of its parts and the pieces we have to work with are conceptual rather than the reality they represent ("the map is not the territory"; Bateson 1972). There is not a holistic isomorphic mapping from reality to the models or concepts we bring to the decision-making process.

We are faced with the immense complexity of both the reality we study and the conceptual information we attempt to work with. It is no wonder that there is confusion in efforts to generate guidance for management. One of many examples is the lack of progress in defining and implementing ecosystem-based management, and, specifically, ecosystem-based fisheries management. Add to this the role of conflicting human values and the situation is nothing short of chaotic. We lack an objective form of management. The choices and interpretation of scientific information to use in management are subject not only to human bias, but to serious errors in logic (Fowler and Smith 2004). As a result, we experience failures in management which have resulted in problems such as global warming, anthropogenic extinction, global pollution, overfishing, and overpopulation (Millennium Ecosystem Assessment 2005, Fowler and Hobbs 2003). Efforts to expand management to include ecosystems (i.e., ecosystem-based management) or management that embraces the biosphere (Lubchenco et al. 1991, Fowler 2003) have failed in spite of a growing volume of literature calling for such action (Guerry 2005, Taylor 2005, Arkema et al. 2006, Steele 2006).

Is our choice of information from the ecological sciences correct for the management of our relationships with the non-human elements of our environment? Are we interacting non-sustainably with other species, ecosystems and the biosphere because we are using the wrong information to guide management?

The prairie dog (*Cynomys ludovicianus*) exemplifies the millions of species that all exhale carbon dioxide – a gas that becomes part of the atmosphere inhaled by other species in one of the interconnections among ecosystems, species and individuals within the biosphere (Photo by Charles W. Fowler, NMFS).

In this paper we argue that our choice of information produced by the ecological sciences for application in management is incorrect and that a correct choice provides the solution to the quandaries we face. This solution is found in the use of natural patterns to guide management. The use of patterns, however, involves understanding that there are only certain products of science (a small subset of what science produces) that lend themselves realistically and directly to guiding management; the bulk of science contributes to the principles that lead to understanding and using patterns. For example, we understand, as a product of science, that the universe is made up of things that are interconnected. Discovering, measuring, experimenting, monitoring, categorizing/classifying, describing, explaining, exposing problems, characterizing, documenting, and predicting are parts of good science. It is crucial that we understand that only very specific patterns will work; the process of identifying these patterns is central to effective management. An objective of this chapter is to show how to identify the patterns most useful in guiding management.

There are three parts to what must be understood in order to make a realistic choice of ecological information to guide management:

I. Natural patterns are integrative. They account for things that are impossible to account for in the current uses of science in management. Such patterns provide an objective basis for management so that we can avoid most of the human elements of decision making that currently cause, rather than solve, problems.
II. There must be a direct link between the natural pattern chosen to answer the management question; there must be consonance in which the information in the pattern has units and circumstances defined by the management question.
III. Avoiding the abnormal is paramount to other values in that abnormal or pathological events or conditions are unsustainable.

These three components to our argument are developed below. A crucial assumption, here, is that we will then manage so that we actually solve the problems before us.

I. Natural Patterns are Integrative

One of the products of science is the conclusion that what we observe has explanation whether we can discover, list and understand all explanatory factors or not. Especially in the case of complex systems (e.g., living or biotic systems), science always provides partial explanation. Given human limitations, complete detailed explanations of what we observe and study will almost undoubtedly never be known. In spite of this reality, many scientists adhere to the belief that if we had infinite resources and unlimited powers of investigation, and observation, we could, in theory, provide a full explanation for any single phenomenon (e.g., Wilson 1998). The common understanding, however, is that there is explanation – whether or not we can ever know it, or document it, entirely. In other words, there are a set of factors, probably infinite in number, that contribute to the formation of what we observe (e.g., the well-recognized ‘butterfly effect’). The phenomena that we observe reflect these factors. Figures 1-3 (and Box 1) help illustrate part of what we mean when we say that patterns are integrative in this way – to fully account for everything.

Figure 1 illustrates the set of both extrinsic and intrinsic factors that contribute to any observed phenomenon. Figure 2 illustrates the complement to Figure 1, showing the feedback from the observed phenomenon to all of the factors that contribute to its explanation. In the case of the fur seal example (Box 1), this would include such things as the effects of fur seals on other species. The origin of any observed phenomenon involve both direct effects and indirect effects, including feedback that works both ways (reciprocity, Fig. 3, exemplified by the effects of resource availability on fur seals but also these resources as influenced by fur seals, Box 1). In being interconnected, all factors, in all cases, can be placed in the center of diagrams such as Figure 3. In other words, every factor (every phenomenon), has its own explanation based on a combination of the universe of factors that varies from phenomenon to phenomenon. If, in reality, there is no connection (direct or indirect) between any two phenomena, that lack of connection would be reflected by its absence in representations such as Figure 3. Bell's theorem (Bell 1964), however, forces the conclusion that no two elements of nature are free from some form of interrelationship in one way or another, directly, or indirectly. Such pervasive interactions are numerous. Humans breath air breathed by bears, dinosaurs, and platypuses. Ground squirrels breath air breathed by humans, saber-toothed tigers and birds. Many of the elements and compounds of the biotic systems of which we are a part flow endlessly from one place to another – exemplified by those carried by migratory species from one part of the Earth to another.

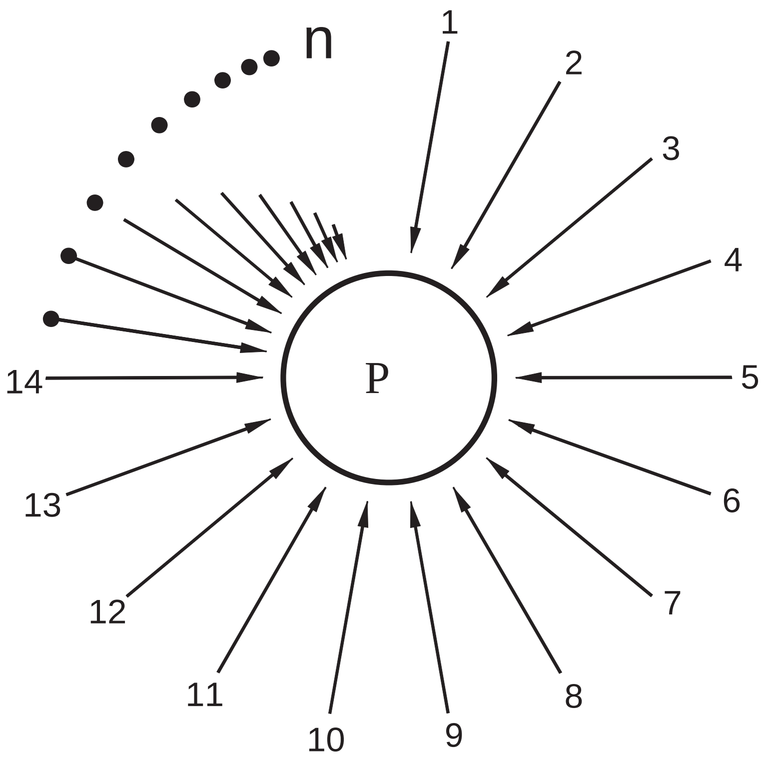


Figure 1. Factors 1 through n (where n → ∞) contribute to the origin and explanation of an observed phenomenon (P). See Box 1 for a specific example.

Box 1.

Towell et al. (2006) observed that the population of northern fur seals (*Callorhinus ursinus*) on the Pribilof Islands are declining. This phenomenon is an example of something that can be observed at the focal points of Figures 1-3. The decline is a product of all contributing factors. It is explained by all contributing factors. For the fur seal decline, these factors can include, to one extent or another, such things as the indirect effects of commercial fishing, the indirect effects of whaling and sealing (past and present), the evolution of competitors, the impacts of pollution and climate change (whether it involves humans or not), the effects of ecosystems, coevolutionary processes, parasites and diseases, predation, genetic changes among fur seals, human economic and belief systems, the effects of marine debris, natural selection at all levels, physical and chemical processes, the behavior and physiology of all species in the fur seal's ecosystem (including the fur seals themselves), population levels of all other species, management decisions of the past, the effects of (and interactions among) neighboring ecosystems (Guerry 2005), evolutionary processes, nutrient cycling, primary production, overpopulation, and the status of depleted/endangered species. This list, of course, is a minute part of the full list of factors operating in the reality to which northern fur seals are, and have been, exposed. Factors contributing to what we see include the intrinsic elements of the fur seal species – its individuals, their physiology, behavior, morphology and organ systems. Each factor, intrinsic or extrinsic, would be represented by one of the arrows in Figure 1 (with interconnections as shown in Figs. 2 and 3). The point here is that all contributing factors are integrated through their influence in the explanation of the decline of northern fur seals. This holds true for any observed phenomenon, including macroecological patterns (patterns among species, Gaston & Blackburn 2000) – all of which reveal limits to natural variation (Fowler and Hobbs 2002). Through this integration, all contributing factors are accounted for in the observed phenomenon.

Regardless of the extent of interrelatedness or the number of interactions, any observed phenomenon is an integration of the full set of explanatory factors behind it. Such phenomena thus represent an accounting of the factors they integrate – always a very complicated set of factors (probably always infinite in view of our knowledge of the interrelated nature of everything; e.g., Bell's theorem). What we see, whether by scientific investigation or otherwise, is emergent from the set of factors that explain it (Morowitz 2002). Some explanatory factors are trivially obvious, and many are subject to scientific scrutiny, documentation, and characterization. Others factors are subject to debate and may never be fully understood or accepted. Still others are beyond the capacity of science to discover and remain unknown. As such, observed phenomena are an integration of complexity well beyond the human capacity to bring them to bear in decision-making. Incomplete consideration of the full suite of such factors is behind the failures of current management. The processes used to consider and account for such factors involves an enormous vulnerability to human limitations; these include the incomplete and limited nature of science, and inability of individuals to think of everything while in their service on advisory panels, commissions, and committees established to try to account for such things in management. The observation, measure, explanation and characterization of integrative phenomena remain within the purview of good science. The phenomena themselves account for complexity.

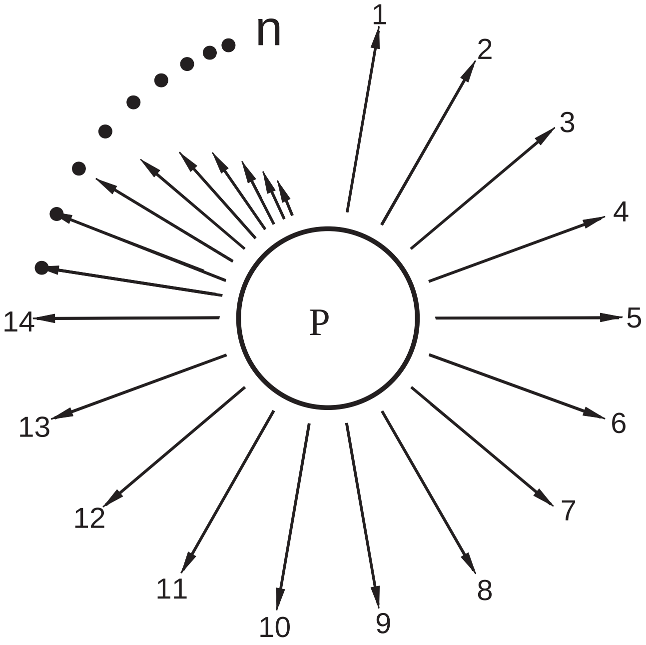


Figure 2. Factors 1 through n (where n → ∞) illustrate the contribution of various aspects of an observed phenomenon (P) to the explanation and origin of other phenomena (both intrinsic and extrinsic).

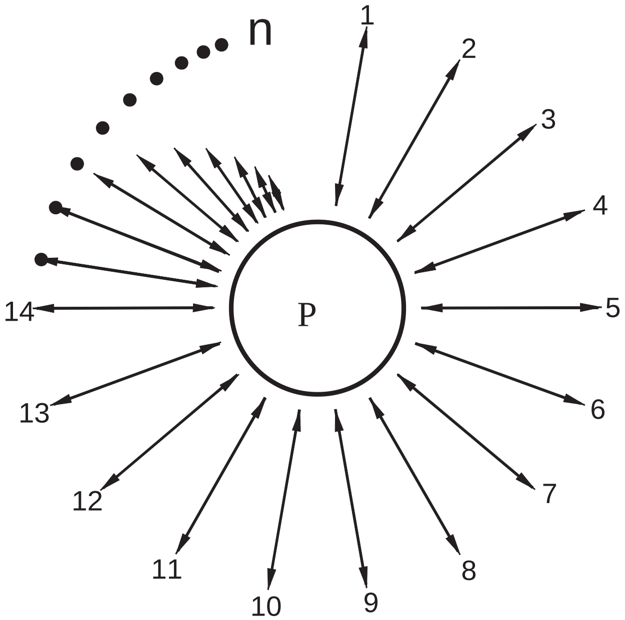


Figure 3. Factors 1 through n (where n → ∞) illustrate the reciprocity of contributions to the explanation and origin of an observed phenomenon (P – a combination of what is depicted in Figs. 1and 2).

Figure 4 illustrates one of the many patterns observed in natural systems – the pattern in which population density is related to body size. Recognition of these patterns is fundamental to the conduct of ecological science. For, example, this pattern can be used in the analysis of food webs to describe communities and ecosystems as complex adaptive systems (Levin 1998) as well as to look at the links between food-web complexity and ecosystem stability.

Along these lines, an important ecological attribute in community ecology and ecosystem dynamics is the maintenance of predator-prey relationships and the observation that food webs are strongly size-based, particularly in aquatic systems (Sheldon et al. 1972). Patterns in body size help link the effects of individual organisms to the relationships and dynamics involved in community and predator-prey interactions. As pointed out by earlier studies, individual body mass can be described by scaling laws (West and Brown 2005, Marquet et al. 2006) and linked to the biological elements of a system to provide estimates of ecosystem properties such as production (Kerr 1974, Boudreau and Dickie 1992, Kerr and Dickie 2001, Jennings and Blanchard 2004).

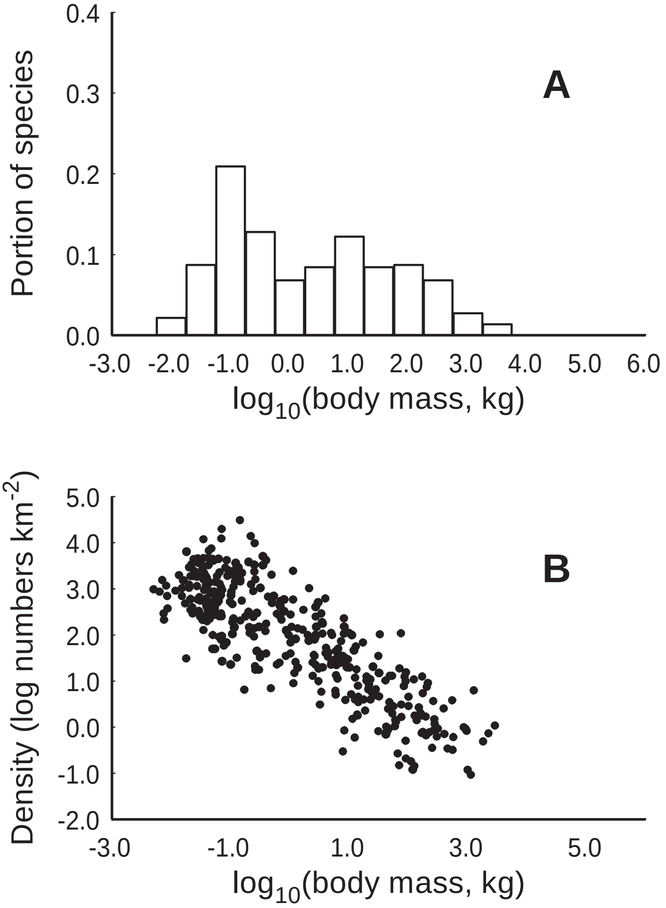


Figure 4. Patterns involving population density and body size. Panel A shows the pattern (frequency distribution) of body size for 368 species of mammals (from Damuth 1981). Panel B shows the pattern *within* panel A involving population density as it relates to body size.

Fundamental to ecosystem structure and function are size-based food webs, patterns in predator-prey body-size ratios, trophic transfer efficiency, and abundance-body-size relationships. In the context of complex food web dynamics models, Brose et al. (2006) emphasized the importance of predator-prey body-mass relationships using allometric scaling theory combined with non-linear bioenergetic models of population dynamics. They showed a clear link between body-size patterns, as an emergent property of natural systems, and the diversity-stability of complex food webs and ecosystem dynamics. Other ecosystem-level properties have been recognized by Sheldon and Kerr (1972) and more recently by others (Link 2002, Nicholson and Jennings 2004). These lead to important ecosystem descriptors useful for assessing the effect of both climate change and fishing pressure on marine ecosystems. However, such principles have not yet been used to link patterns to policy. Our point is that these principles, along with yet unknown principles, would be brought directly to bear in setting policy through the use of patterns that integrate (Figures 1-3); such principles are among the set of factors involved in the explanation/formation of an observed phenomenon (e.g., Fig. 4). All such factors count in what is integrated in a natural pattern. Another example is the relationships between structure and diversity in food webs (Jennings et al. 2002, Cohen et al. 2003) that includes recent developments in scaling theory and macroecology (Jennings and Mackinson 2003, Belgrano et al. 2002, Li 2002) applied to marine systems. All such interrelationships and dynamics are integrated in observed patterns through the variety of ways they contribute to such patterns.

Steller’s sea lion (*Emetopias jubatus*) and the fish it consumes are examples of predator/prey interactions that typify marine ecosystems in ways that contribute to the formation of patterns and exhibit patterns themselves (Photo courtesy of, and copyright by: Larry Hobbs, Inland Whale).

In the course of ecological research, a framework of size-based food webs will allow a better understanding of the abundance-body-size relationship for communities that share and compete for a common energy source (Cyr 2000, Ware 2000, Cohen et al. 2003, Brown and Gillooly 2003, Brown et al. 2004, Maxwell and Jennings 2006), as well as the links between biodiversity and ecosystem functioning (BEF, Naeem 2006). For example, changes in species composition and interaction strength due to co-evolutionary processes at the local and regional level can have drastic indirect effects or a larger-scale impact due to the loss of important system properties such as demographic processes. Discovering such connections is part of ecological science that leads to understanding basic principles, explanation and prediction. These dynamics contribute to the explanation of observed patterns (Figs. 1-3). Patterns in food webs can provide guidance for specific management issues when the pattern is consonant with a management question as developed below.

In leading up to the concept of consonance, it is to be noted that a pattern, such as that shown in Figure 4A, is never as simple as might appear on the surface. Within the pattern of Figure 4A is a clear relationship involving population density (Fig. 4B, Damuth 1981). When examined in even greater detail, another internal pattern with respect to trophic level can be seen (Peters 1983, Fowler 2005). All such factors are integrated (accounted for) in the overall, more general, pattern. An explicit representation of such patterns opens the option for overtly accounting for correlative factors such as those observed between density and body size in Figure 4B, or those observed in correlative relationships involving both body size and trophic level (Fowler 2005). Correlative relationships are an important element of finding consonance between management question and guiding pattern, the topic of the next section.

II. Consonance between Management Question and Pattern

A clear distinction is to be drawn between questions that involve science and questions that involve management. Science involves such things as understanding, explanation, documentation, predicting, monitoring, categorizing, observing, characterizing, measuring, and exposing problems. Management involves what we do, our action, and our objectives or policy. Specifically, management involves humans in our action, objectives and policy. Science questions, then, involve words such as “why,” “how,” “when,” “where,” and “what.” Management questions often involve similar words but always with the element of “should.” For example, the management question “What is a sustainable harvest of fish from the Gulf of Mexico?” implies that the answer will be converted to objectives, action and policy to achieve that level of harvest because we “should.”

There must be a direct match (consonance) between management question and the pattern that provides guidance. This means that there must be common units, common circumstances, and common logical typing. With consistent logical typing, we not only avoid mixing apples and oranges, we do not mix apples and fruit (Fowler and Smith 2004). The following paragraphs explore these three aspects of consonance – consonance being the match, isomorphism, congruence, or common ground between the management question and the corresponding science question so that we can find the appropriate pattern for use in guiding management.

The coyote (*Canis latrans*) is an example of a species within terrestrial food webs that have species that consume prey at a variety of trophic levels – a dynamic that counts among the factors that contribute to food-web patterns (Photo courtesy of, and copyright by: Bruce Fowler).

The matter of common units is quite straightforward. We can, for example, address the management question: “What is a sustainable harvest of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea?” as an important question in the management of commercial fisheries in the Bearing Sea ecosystem. In part, the question can be framed in terms of either biomass or numbers. If we work with biomass, the question gets refined to: “How many metric tons of pollock can be sustainably harvested from the eastern Bering Sea?” The answer to the question must be phrased in terms of biomass (e.g., metric tons), presumably as an annual harvest. These factors lead to further clarification of the question by expressing it as: “How many metric tons of pollock can sustainably be harvested annually in the eastern Bering Sea?” The units of biomass per year are specified by the question, requiring that science provide information in those units. One aspect of units, however, is often neglected in cases like this: we humans are introducing ourselves as a predator on pollock by harvesting biomass from this species. We compete with the other predators that consume pollock. What is sustainable consumption in units expressed as biomass consumed per predator? From an ecosystem prospective, then, the question we are asking must be refined in another step: “How many metric tons of pollock consumption (harvesting) per predator per year are sustainable in the eastern Bering Sea?” This specifies science that provides information in terms (units) of biomass consumed per year per predator as pertinent to the eastern Bering Sea.

Note that circumstances involving location are inherent to the question in all formulations above – the eastern Bering Sea ecosystem is specified in each case. This means that the science brought to bear in addressing the question must provide information specific to the eastern Bering Sea. Given the geographic size of this ecosystem, it also specifies units of consumption related to area (e.g., biomass consumed annually per square kilometer). However, there is more to the complexity of this system than its area. There is its location, exemplified by its latitude. There are the environmental circumstances of climate and weather, circulation of currents, salinity, depth and primary productivity. There are evolutionary/coevolutionary dynamics in the history of this ecosystem. Extinction has contributed (Fowler and MacMahon 1982) to the character of this ecosystem. These are a very few of the circumstances and conditions inherent to the structure and function of ecosystems. Mean trophic level, turnover rates, diversity and other features of a ecosystem (Link et al. 2002) should also be accounted for in management. All these factors contribute to the phenomena observed in nature and, in particular, the observed patterns in the eastern Bering Sea. As a result, patterns of predation in the Bering Sea take on some of the consonance we need between the management question and the products of science that inform us so as to provide guidance. Inherent to the existence of such patterns is an accounting for the complexity involved (Figs. 1-3). However, as with units, circumstances can be dealt with more overtly than simply knowing that they are reflected in natural patterns. Science may discover correlative relationships within the more general patterns that directly reflect circumstances such as latitude, season, or depth. The formulation of questions regarding such patterns involves the posing of scientific questions which are guided by (defined by) the underlying management question.

It bears noting that our management question, here, involves a single-species quality – one single species (humans) harvesting another single species (pollock). It is ecosystem-based, however, in that the question is phrased with respect to a specific ecosystem. However, this is only one step toward approaching the question from an ecosystem-based perspective. As we shall see shortly, the pattern that provides guidance is fully integrative of ecosystem considerations (Figs. 1-3).

Thus, we proceed toward management by a series of steps in which the management question gets refined. It is refined by factors that conventionally are subject to debate and politics. Such deliberations are usually polarizing in conventional management. However, in pattern-based management, when such issues are raised, they add to the factors to be examined in search for correlative pattern. The raising of such issues is part of the refinement process of systemic management. In systemic management the raising of such issues is confined to the role of refining questions and not allowed as political arguments in favor of a particular policy or objective. In addition to the patterns involved, and recognized in macroecological studies, this refinement involves asking a management question in terms of circumstances. Continuing with our example we might ask: “How many metric tons of pollock consumption (harvesting) per predator per year are sustainable at the latitude, biodiversity, and mean trophic level of the eastern Bering Sea, knowing that pollock are cannibalistic?” If there are correlative relationships among ecosystems that show predation to be related to such factors, they can be dealt with overtly. Otherwise, they are inherent to the more general pattern, just as are all of the influences humans bring to our world. Such human influences include overpopulation, overfishing, pollution, carbon dioxide production, economic systems, marine acidification, belief systems, and extinction. All such factors are reflected in natural patterns (Figs. 1-3) to, thereby, be taken into account in the use of such patterns.

The business of avoiding the confusion of ‘apples and fruit’, or logical typing, may be a bit more foreign to our ways of thinking about management information than are circumstances and units of measure. Logical typing began to enter our example above at the point where we note that we are imposing ourselves in the eastern Bering Sea as a predator and ask about sustainable consumption levels from any resource as reflected by the predators feeding on that resource. Logical typing involves the matter of part and whole; complex systems are composites of parts and wholes. Our question on the sustainable level of pollock consumption is a question about our (the human) *part* of consumption and its sustainability; consumption by all predators is a whole with parts about which we are asking our management question. In the extreme, if we confined ourselves to the whole, we could continue with the paradigm of maximum sustainable yield (MSY) and claim we can take all of the production stimulated through the reduction of the population of a resource species to elicit a density dependent response. However, the question is really about our role as a predator in the system and the sustainability of our *part* in the consumption of production by predators. Care must be exercised here, as the fate of production involves several categories, only one of which is consumption by predators. Of all of the interactions and relationships involved in ecosystems, this is the category of such relationships to which our management question is addressed. We are trying to determine what is a sustainable *part* of the predation process – keeping in mind that there are likely to be further sub-categories that involve even more consonance made apparent by extended refinement of the management question.

The issue of logical typing is clear, then, when we realize that measures of production are no more than that: measures of production. Our management question is a question about consumption (often called ‘harvest’ or ‘take’ in fisheries management). Production is production and consumption is consumption – two different things. They are so different as to be of different logical types; consumption is *part* of the fate of production and obviously not production. We can thus phrase the question in terms of our *part* of the production to be consumed by predators, rather than assume that we can increase production (via population reduction and stimulated density dependence in resource populations) and then can harvest all of the increase. Our question becomes one of the sustainability of our *part* of consumption – consumption by humans as one of the predators. Some production must go to replenishing the resource’s population to offset mortality. Some of the mortality contributes to decomposition and maintenance of decomposer populations as inherent components of any ecosystem – elements to be maintained in any ecosystem-based form of management. The whole of production *per se*, therefore is not an option for informing and guiding management. Even an unspecified part of production fails to achieve the consonance we are after as we seek to know how we can compete sustainably with (i.e., without out-competing, and causing depleted or endangered status among) other species that are consumers. The categorical designation of the focus of our management question, therefore, is our part of consumption, and specifically the category of consumption involving predation (knowing full well that it cannot exceed the total production as the ecosystem will not survive such excess).

Coral reefs, such as the Aitutaki Reef in the Cook Islands, exemplify numerous symbiotic interactions that are part of the interconnectedness of ecosystems exhibiting and contributing to the formation of empirical patterns (Photo courtesy of, and copyright by: Larry Hobbs, Inland Whale).

We can now refine our management question further: “How many metric tons can sustainably be harvested annually as our part of the predation on pollock, a cannibalistic species, at the latitude, and with the biodiversity, and mean trophic level of the eastern Bering Sea?” As should be increasingly obvious, the role of human limitations changes. In conventional management these limits are ignored by design in the decision-making process. These limits are inherent to the process of translating relevant, but partial and non-consonant, information to consonant guidance. This leads to errors in policy and management. In pattern based management, our limits become expressed in two ways which differ greatly from the way they interfere in conventional management. First is our inability to ask all management questions. Second is our inability to refine management questions to account for every detail. The first limitation is inherent to all forms of management. In the second case, ecological sciences are relied upon to find the primary correlative patterns within more general patterns. These will emerge in responses to management concerns wherein the unrealistic compromises of debate in conventional management become replaced with matters for scientific investigation in examining empirical patterns.

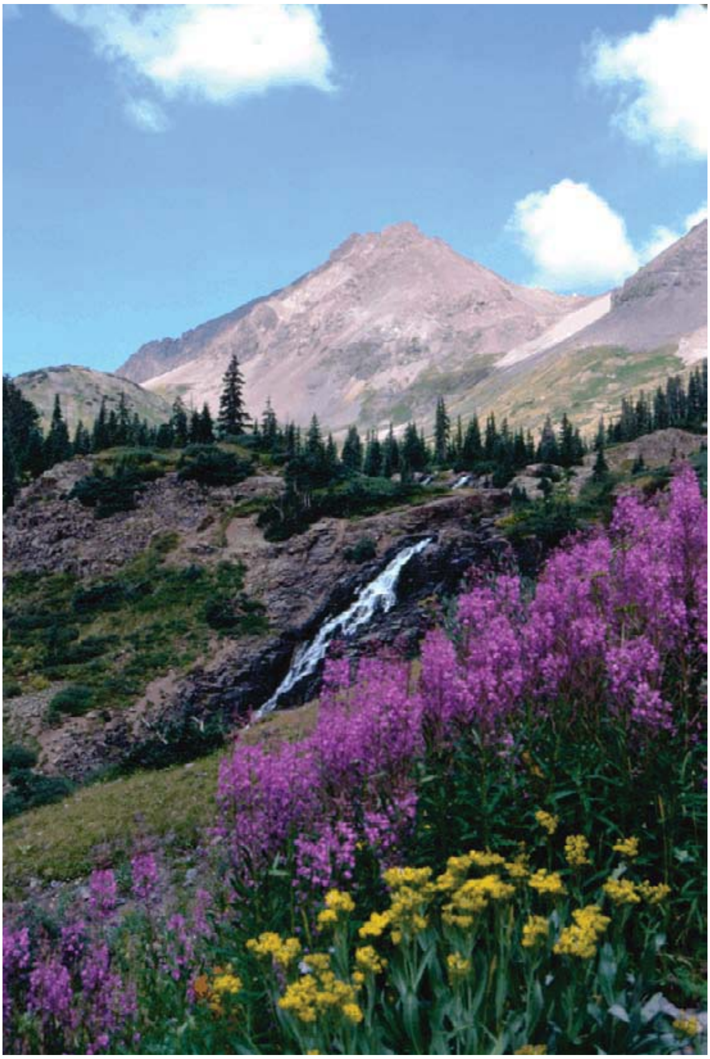
III. Avoiding the Pathological is Paramount

Human values, belief systems, and past and current actions through conventional management are among the factors that contribute to what the ecological sciences discover, describe and document in today's world. They count as parts in the explanation of observed phenomena, including the problems science exposes (Figs. 1-3, Box 1). Most of today's literature on ecosystem-based management (or management in general), expresses a strong bias toward bringing human values into the arena of policy and decision making. The involvement of stakeholders in the decision-making process has been seen as one of the primary objectives of the management process (e.g., Phillips and Randolph 2000, Arkema et al. 2006). Certainly, the value attached to involving stakeholders in making decisions and setting policy has been fundamental to what we have been doing. More generally, an objective form of management is often rejected as impossible or seen as no more than a myth (e.g., Norton 2005). Do these assumptions function as important components contributing to the problems before us?

In view of the problems that confront us today (Millennium Ecosystem Assessment 2005), there is reason to see today's problems as problems involving our belief systems. As such, there is strong basis for seeking an objective basis for setting policy, making decisions, and setting goals. We need a way forward in which stakeholders, scientists, and managers are prevented from participating in the conversion of scientific information to guidance, especially when that information is merely relevant and always partial rather than consonant at the outset. In view of the contribution that human values and limitations contribute to the problems observed today, we need a way to account for them. We argue here that pattern-based decision making provides a way to bypass politics, debate, and the conflict of human values. Human values and belief systems are accounted for in observed patterns (Figs. 1-3). Pattern-based decision-making involves avoiding the pathological; the abnormal or pathological are made obvious in patterns consonant with specific management questions. Such patterns establish what is normal and outliers appear as pathological circumstances to be avoided. These patterns are integrative so as to remove human involvement in translating relevant information to policy – in converting partial information to guidance.

We are fully aware that there is a value involved in adopting management that has the overarching goal of avoiding the abnormal or pathological. This is a value that transcends or surpasses the values we currently bring to management – values that either over-express human interests (anthropocentrism – Roszak 1992) or the welfare of the non-human (biocentrism – Aplet and Johnson 1993). The value of sustainability to avoid the abnormal is a value about the process of decision-making rather than part of the decision making (another matter of logical typing). The anthropocentric is placed in balance with the biocentric. An objective form of management eliminates the influence of human values other than those that underlie management as a whole – the value of avoiding the abnormal to achieve sustainability. In this way, the value of sustainability transcends other values.

When humans are outliers in patterns consonant with specific management questions, we need to undertake changes to solve the problem – eliminating the abnormality. When other species (ecosystems or the biosphere) are shown to be pathologically abnormal we need to take actions to avoid human abnormality as human influence contributing to the non-human problem – always elements counting among the factors contributing to what we see (Figs. 1-3). Thus, if we use known ecosystem metrics (e.g., biodiversity and other factors exemplified by those mentioned by Link et al. 2002), and find that an ecosystems is abnormal, we look for cases of human influence that is abnormal and potentially exacerbating the problem. Management should alleviate human abnormalities with the knowledge that they are contributing factors, in various ways (Figs. 1-3), to the ecosystem problem. Some of these effects may actually be mitigating effects. As such, implementing management that confines commercial harvests of pollock to a normal level of consumption is not to be done simply because of any contribution it makes to the decline of northern fur seals (Box 1), but because of all such interactions and because of all of the effects the abnormal consumption rates have on all components and processes – not only in the eastern Bering Sea, but the biosphere as a whole.



Ecosystems of the world, such as this montane system, do not lend themselves to full isomorphic mapping to any model, yet their complexity is part of what is integrated and accounted for by the reductionistic patterns we observe insofar as they are consonant with specific management questions (Photo courtesy of, and copyright by: Bruce Fowler).

This perspective helps bring the objective nature of pattern-based or systemic management into focus. The health of any species in an ecosystem is of no more (nor less) importance than is expressed in its being a part of the ecosystem. The health of the ecosystem becomes a matter of importance held in balance with the health of individual species – specifically that of the human species. The value we place on social and economic concerns comes into focus as part of the suite of factors that contribute to what we see in today's world – specifically the problems that have been exposed by science. The economic hardship of avoiding the abnormal is a direct reflection of the degree to which economic factors contribute to the abnormal.

Thus, although avoiding the abnormal involves a value, it is a value that eclipses other values. The debate, involvement of stakeholders, meeting of panels, establishment of special committees, and reorganization of various agencies we now undertake to achieve ecosystem-based management can be seen as not only unnecessary, but sources of misdirected advice. Of the wide variety of information produced in ecological research, only that which results in the discovery, documentation and characterization of patterns consonant with specific management questions is pertinent in a useful way. The remainder of science retains its importance in demonstrating things that we already know – the elements of nature are interconnected, various relationships are involved in these interconnections, what we observe is emergent from the complexity of contributing factors, and the complexity of nature prevents our understanding everything. Such principles are among those that need to be accounted for in management – and are through the use of patterns consonant with management questions.

A Single-species Example

Figure 5 is a diagrammatic representation of a natural pattern exemplifying the products of science that can guide management in a way that simultaneously reflects, and accounts for, the other products of science. It is related to the question we have been refining in the paragraphs above. It is the pattern observed in consumption rates by predators that feed on walleye pollock as it would have been used to manage harvests of pollock in the early 1980s. Consonance between this pattern and the management question is achieved insofar as the pattern involves 1) units of biomass consumed per predator, per year, 2) applies to the eastern Bering Sea (is integrative of all of the factors involved in the complexity of that system, and reflects the history and circumstances of the early 1980s), and 3) overtly accounts for the fact that humans are a large mammal (is a pattern involving measurements for large mammals – size being a factor in ecosystems as shown in many macroecological patterns; e.g., Fig. 4, Peters 1983). It accounts for the fact that pollock are cannibalistic simply because pollock are cannibalistic and therefore one of the factors (here, an intrinsic factor) involved in the explanation, origin, or emergence of the pattern.

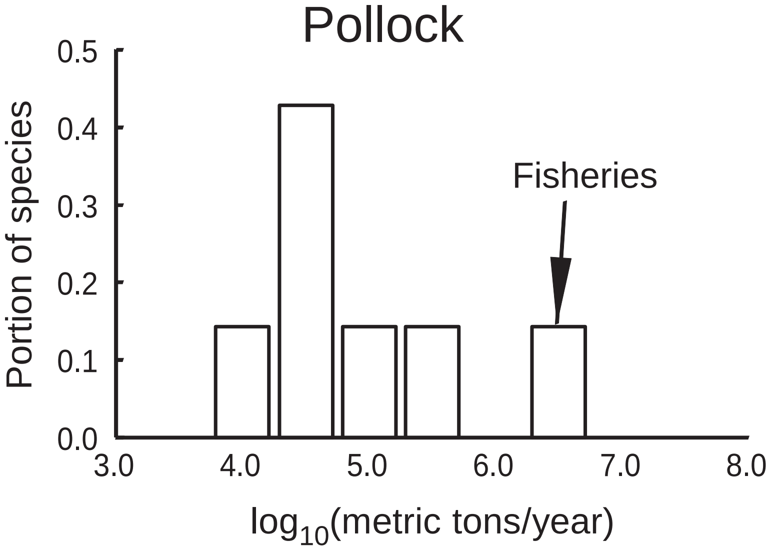


Figure 5. The pattern of consumption among seven species of large mammalian predators (including humans) for walleye pollock in the eastern Bering Sea (Fowler 2003).

Thus, for management, the important point regarding the pattern reflected in Figure 5 is that it establishes a Bayesian-like integration of complexity (Figs. 1-3; Fowler 2003), so as to establish the probability density of sustainable annual consumption of pollock (a cannibalistic species) per predator for large mammals. The integration involved in this pattern includes all ecosystem effects (known or unknown, e.g., Box 1) so as to make the pattern, not only an ecosystem-based source of guiding information, but also biosphere-based, and (in the extreme) reality-based (accounting for the universe of contributing factors). This permits the measure of abnormality of individual measures, such as that for commercial fisheries as they were managed in the early 1980s. It simultaneously begins to show evidence of what was most sustainable (or least abnormal) at the time to which the estimated consumption rates applied, that is, what worked in the system under the circumstance to which it was exposed (climate, global warming, fishing..... – the complexity of circumstances).

How do we use a pattern such as that shown in Figure 5 to establish a management objective? In other words, how do we use this information to answer the management question about a sustainable harvest of pollock? The products of science must result in identifiable objectives in order for them to be implemented (with an emphasis on the quantifiable; Fowler 2003). Biodiversity has been a core element of concern in management (Smith 2000). Figure 6 shows what would have been the harvest of pollock if we maximized the biodiversity within the pattern shown in Figure 5. Maximized biodiversity (the peak of the curve in the bottom panel of Fig. 6) offers an alternative to the mean, mode, or the 0.95 confidence limit of the pattern, as a reference point or objective for management. In this case, the harvest estimated to maximize biodiversity would have been less than 6 percent of the harvest taken in the early 1980s.

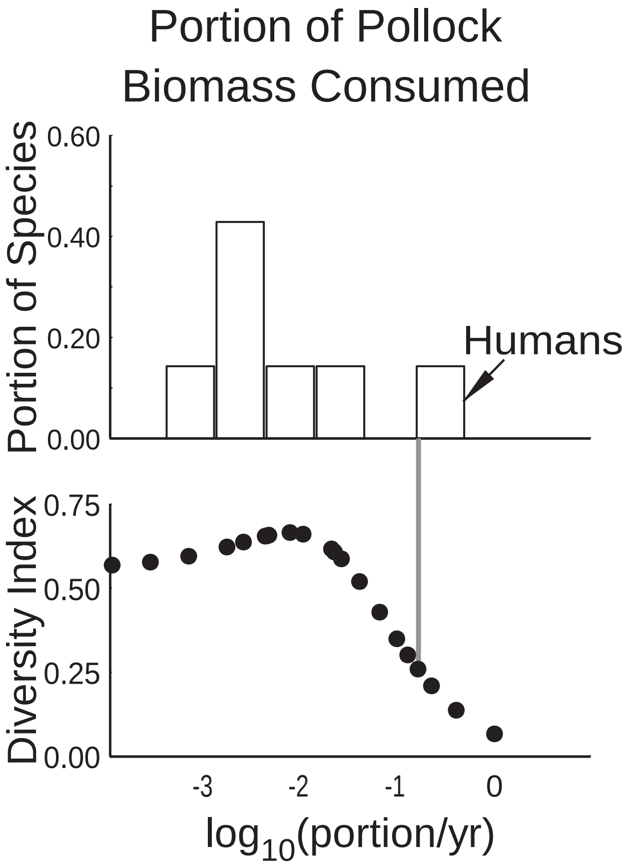


Figure 6. The pattern of consumption from Figure 5 (in units of portion of the standing stock of pollock biomass consumed) shown with measures of the biodiversity (Shannon Weiner information index; Pielou 1969, Krebs 1972, Nielsen 2000) plotted in the bottom panel as a function of the position of the commercial harvest rate (i.e., consumption by humans).

To apply pattern-based management or systemic management (Fowler 2003) to the question of pollock harvests today, we need current estimates of the consumption rates for all the large mammals of the eastern Bering Sea to reflect current circumstances (effects of global warming, pollution, fishing, and the effects of non-human factors exemplified by climatological cycles).

An Ecosystem Example

Figure 7 (top panel) illustrates a pattern similar to that shown in Figure 5, here, however, related to the management question posed at the ecosystem level: “How many metric tons of biomass can sustainably be harvested annually as our part of the consumption by large mammal predators in the eastern Bering Sea?”

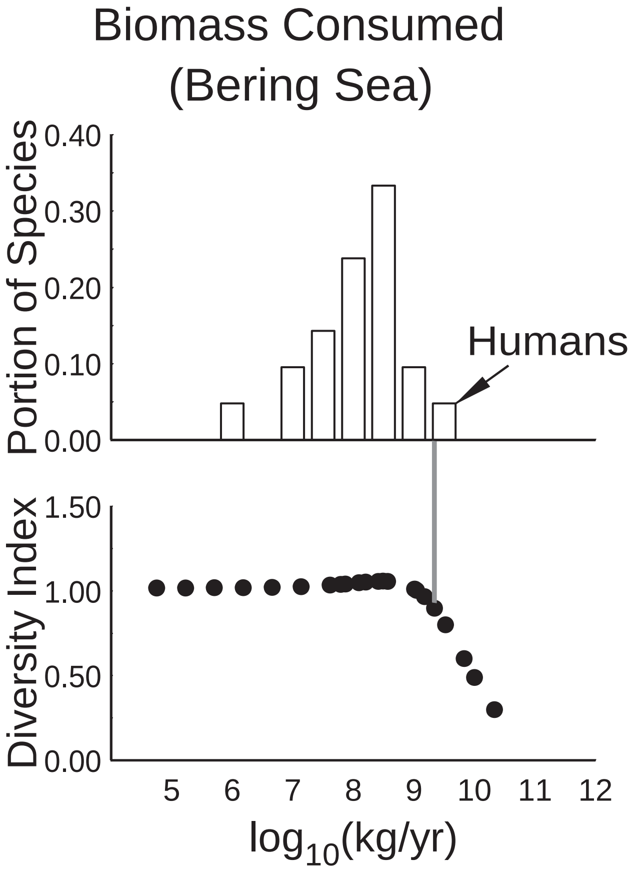


Figure 7. The pattern of consumption by 22 predatory species (including humans) in the eastern Bering Sea, shown in the top panel as the frequency distribution of consumption rates and in the bottom panel as biodiversity expressed as a function of the consumption (harvest rate) by humans (commercial fisheries), similar to the bottom panel of Figure 6.

The bottom panel of Figure 7 shows the maximization of diversity to establish a harvest of about 308,000 metric tons annually for the early 1980s. The actual harvest was over seven (7.14) times larger than that which would have maximized biodiversity.

In this case we have an ecosystem-based set of guiding information; the pattern integrates all ecosystem effects (Figs. 1-3) for an ecosystem-level question. Full scale ecosystem-based management would address all ecosystem-level questions. These would be exemplified by: What portion of the Bering Sea ecosystem should be free of the direct effects of the human harvest of resources (e.g., left as marine protected areas)? How many species should we be harvesting? What is a sustainable species composition of commercial harvests (i.e., How should we allocate our harvest of resources across species?); again, such multispecies questions can be addressed by natural patterns as shown by Fowler (1999). We are limited only in our ability to ask such questions and then in our ability to define and conduct the science to find the empirical pattern consonant with each question.

DISCUSSION

As with all human endeavor, the sciences (including the ecological sciences) are confined by their reductionistic qualities. Reductionism is one of the reflections of human limitations. Conventional management has been the victim of erroneous translations of reductionistic scientific information to management advice. In fisheries management this kind of misdirected reductionism is exemplified by the use of information about production (population growth rates as a function of population size) to inform management when the management question involves sustainable consumption rates. This mistake originated in the 1930s when J. Hjort, M. Graham, M.B. Schaefer and others simply equated production and consumption in the origins of the MSY approach to the management of resource harvesting (Smith 1994). Systemic, or pattern-based, management requires that there be consonance between management questions and informative patterns so that such errors are avoided. Systemic management takes advantage of the limits of science by providing integrative reductionistic focus to avoid the mismanagement of conventional approaches. The refinement of consonance between a focused management question and observed pattern involves healthy reductionism in taking advantage of integrative reductionistic patterns. Patterns of information isomorphic to carefully posed management questions make up the portion of scientific information useful in decision-making, setting policies, and establishing goals or objectives. Research characterizing these patterns thus constitutes the ‘best available scientific information’ (NRC 2004) as the basis for management. The remaining aspects of science contribute to knowing that patterns reflect complexity and the identification of some (but probably never all) of the elements of that complexity.

Pattern-based management, then, circumvents politically-based translation of partially related, incomplete, and poorly understood scientific information. The misdirected reductionism of current practices is replaced by guiding patterns that are reductionistically defined by carefully crafted management questions – always asked in terms of what we (humans) can do sustainably. These patterns form the basis of management that is evolutionarily enlightened; such patterns are integrative of processes including natural selection at both the individual and the species level (Fowler and MacMahon 1982). Emergence involves the self organizing aspects of complex ecological systems (Solé and Bascompte 2006). It involves evolutionary processes among the factors contributing to the phenomena we observe, and specifically the patterns that illustrate the limits to natural variation (Fowler and Hobbs 2002). These patterns are nature’s Nash equilibria (Fowler 2003) in their integrative nature to account for the hierarchical nature of the system in which we are trying to be a sustainable part. Management based on patterns is adaptive management (Holling 1978, Walters 1986) extended through the realization that what we observe is the result of nature’s trial and error processes – including selective extinction and speciation (Fowler and MacMahon 1982).

Cooperative feeding, such as that of humpback whales (*Megaptera novaengliae*), and bird/whale feeding interactions involve behavioral interactions that contribute to the formation of empirical patterns (Photo courtesy of, and copyright by: Larry Hobbs, Inland Whale).

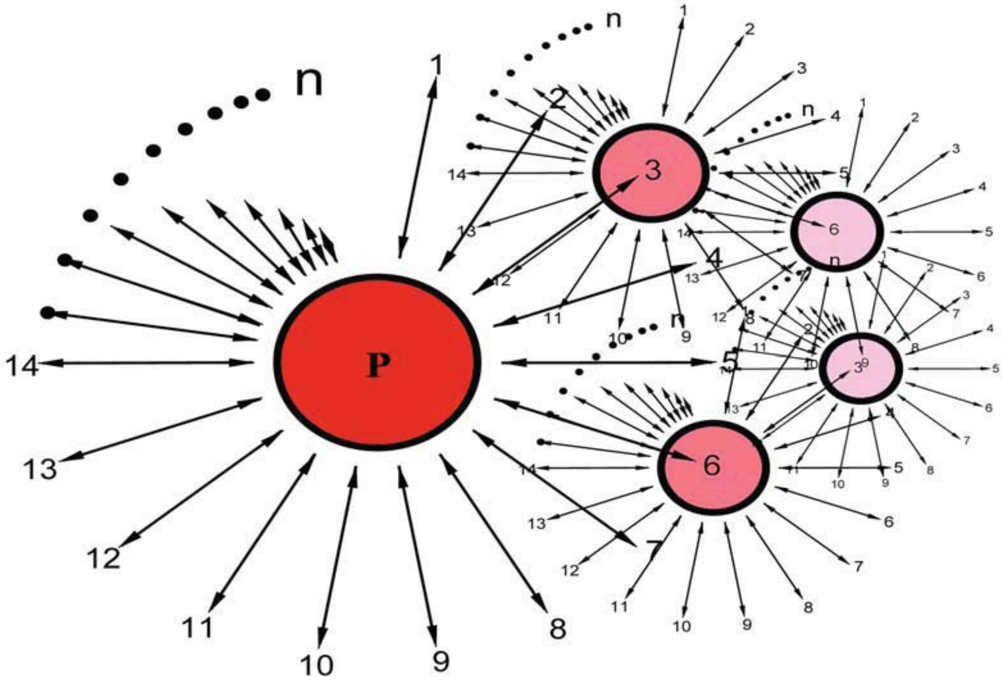


Figure 8. Indirect effects are part of all complex systems such that any phenomenon (P – dark red) interacts with others (light red; and feedback to itself) through reciprocity that follows the pathways of interactions among other parts of the system to involve higher-order indirect interactions (light lavender). Such interactions involve nth-order interactions (where n → ∞) never possible to capture in any model other than emergent patterns.

With one exception, meetings, debate, and political conflict that invites (and depend upon) the intervention of human values are rendered unnecessary when we take a consonant pattern-based approach to bypass the process of translating/converting partially relevant scientific information to management. That exception involves interdisciplinary efforts to pose realistic management questions and subsequent research strategies to reveal the consonant pattern. Stakeholders need to participate in that process, as well as be involved in management action. They should not be involved in decision-making the way they are today. With stakeholder help, management questions must be posed so that they define the needed science: the research needed to discover, characterize, and document consonant patterns. Many of these patterns are macroecological when it comes to defining a sustainable role for our species in the world's ecosystems and biosphere. Without the meetings and debate currently involved in processes using, and depending on, misdirected reductionism, there will be tremendous monetary savings in solving and preventing more costly problems – costs that are not only economic but, more importantly, intrinsic to our survival as a species (e.g., extinction).

Part of the challenge in management at the ecosystem level involves accounting for indirect effects. The burden of proof is reversed in systemic management through our understanding that things are interconnected – relationships exist among all things. The indirect interconnections are illustrated in Figure 8, and, as described above, are part of what gets integrated (and accounted for) in natural patterns. Indirect effects involve higher-order interactions as chains of indirect effects and feedback – all part of what contributes to what we observe. Systemic management encompasses ecosystem-based management and part of ecosystem-based management is ecosystem-based fisheries management. Not only can we address questions concerning the harvest of an individual species within an ecosystem (Fig. 6), but we can address ecosystem-level questions such as "How many metric tons of biomass can be sustainably harvested annually in the eastern Bering Sea?" (Figure 7).

There are many other applications of systemic management – all pattern-based. Examples of a few have been published. An overt treatment of selectivity exemplifies management that fully accounts for evolution, natural selection, and genetics (Etnier and Fowler 2005). Multi-species approaches (Fowler 1999) are part of systemic management, as are biosphere approaches (Fowler 2002); there are applications at all levels of hierarchical organization within biotic systems (Fowler 2002). Establishing the optimal spatial distribution of resource consumption (Fowler 2002) as well as the location and size of marine protected areas are parts of the process of systemic management.

Thus, following the work by Fowler (1999, 2003) on systemic management, we argue that the use of a place-based macroecological analysis of emergent patterns such as species abundance, body size distribution, and biomass consumption can be used to describe the robustness and strength of species associations at the ecosystem level. Over different spatial and temporal scales, patterns serve as a tool to link complexity in natural systems to management. These empirical patterns, once validated, may then be linked to atmospheric and hydrographic forcing, to provide guidance toward sustainable fisheries management that includes ecological knowledge. The basis for using a macroecological approach to systemic management is that, conceptually, ecosystem complexity involves first principles that are reflected in patterns. Macroecological patterns can be used to calculate, for example, the constraints in species richness and ecosystem functioning thus providing generalities across systems that can be used to identify the scientific information that accounts for socioeconomic factors in the implementation of an ecosystem-based management approach. Socioeconomic factors count among all of the factors that are accounted for in the formation of observed patterns.

SUMMARY

The ecological sciences (and the sciences in general) produce a great deal of discovery, understanding, prediction, and characterization. Out of these products of science, only the discovery and characterization of patterns consonant with management questions provide guiding information; the remaining products of science contribute to the understanding of why this is the case. Systemic management is pattern-based and makes use of patterns to avoid the pathological or abnormal with the overarching goal of sustainability. Patterns that are consonant with specific management questions are integrative of the complexity needed to ensure that they are not only ecosystem-based but are also reality-based. Consonant patterns are those that are congruent with, share identical units with, and are isomorphic with the management question to which they are matched. The emergence of these patterns make their integrative qualities inherent – the effects of humans with attendant socioeconomic factors and their influence, our history and belief systems, and the effects of our technology are all included in this integration.

Systemic management replaces current or conventional management where human limitations lead to the mistakes behind the problems science documents. Systemic management, as pattern-based management and pattern-based policy making, adheres to the tenets of management requiring that we avoid the abnormal, achieve sustainability, and proceed with approaches that account for ecosystems and the biosphere. The full arena of ecosystem-based management is a part of systemic management; in particular, ecosystem-based fisheries management is a part of systemic management.

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Chapter 2

RESPONSES OF MICROBIAL POPULATIONS AND PROCESSES TO PULSES OF PRECIPITATION IN SEMIARID FOREST ECOSYSTEMS

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ABSTRACT

Understanding how abiotic factors regulate soil microbial activity is key in understanding the responses of terrestrial ecosystems to anticipated climate change. Soil microbes catalyze biogeochemical reactions and the exchange of nutrients between heterotroph and autotroph organisms, as well as between the soil and atmosphere. Semiarid forests are driven by "pulses" of precipitation (episodic and irregular events of precipitation) which activate soil microbial activity and their processes. Our knowledge on the functioning of semiarid forest ecosystems in response to pulse events has increased substantially over the last decade. However, a comprehensive paper synthesizing this literature and making conceptual progress at global scale is yet missing. This paper is a review of the current knowledge on microbial populations and their processes in forest semiarid ecosystems after pulse events. First, we briefly describe distribution and abundance of soil microbial biota in these systems. Second, we review ecosystem processes, and how they are regulated by microbial communities. These ecosystem processes include soil respiration, carbon and nitrogen dynamics and decomposition. Third, we address the effects that climatic change may exert on these populations and processes. The effects described are increased CO2 concentrations, elevated temperatures and changes in precipitation regimes.

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Keywords: soil microbial communities, ecosystem processes, C and N cycle, gobal change

INTRODUCTION

Semiarid and arid ecosystems account for more than 35% of the Earth's land area [1]. Water availability is the main limit to the net primary production of semiarid ecosystems and its availability mediates the responsiveness of communities and ecosystems to global changes [2]. These systems are driven by episodic “pulses” of precipitation which activate biological activity [3]. Responses to such pulses differ between life forms, where soil microbial populations are the first to respond and woody C3 species the last ones. An increasing body of literature has arisen recently studying aboveground responses to pulses of precipitation [4-7] but to date, information on the quantitative effects of water pulses on belowground processes is relatively scarce [8], probably because of methodological limitations.

The aim of this paper is to review our current knowledge on i) the distribution of soil microbial communities in semiarid forest systems and their responses to pulses of precipitation, ii) how pulses influence microbial processes and iii) how are these relationships expected to change under climate change. Reviewed studies were selected from exhaustive searches on Web of Science and Cab abstracts. We intended to use only those papers which were explicitly testing the effects of pulses of precipitation. When no studies with this focus were found, We used papers on longer term dynamics, or hypothesized about the consequences of the processes described in the text.

DISTRIBUTION AND ABUNDANCE OF SOIL BIOTA

Soil environmental heterogeneity is an important factor determining microbial distribution and provides differences in the quality of the soil as a habitat for microorganisms. This heterogeneity mainly consists of differences between mineral and organic soils, soil organic matter (SOM) quantity and quality, textural class, pore spaces, pH, cation exchange capacity (CEC), soil water, soil aeration and soil temperature [9]. Some of the most unique properties of semiarid soils constraining the activity of soil microbes are i) that they tend to be very well aerated at the expense of extremely low water potentials, which impose strict controls on soil microbial communities biomass; ii) that these low soil water potentials also diminish the productivity of the system, and therefore the organic horizon tends to be very thin or nonexistent; and iii) that although soil temperature may vary with different kinds of systems (e.g.: Mediterranean vs Great Basin ecosystems), there is a high fluctuation between day and night air temperature. This fluctuation is more important in the top soil, which is more influenced by air temperature.

Substrate or resource is probably the most important factor regulating the abundance and distribution of soil microbial populations. Changes in the distribution of autotrophic organisms modify the distribution of the substrate. Two main different types of resource distribution have been described for desert ecosystems. 1) In semiarid grasslands, we find a near-random distribution of soil resources which leads to a near-random distribution of soil microbes [10]. 2) In woody vegetated semiarid systems, resources follow a patchy distribution which creates spatio-temporal heterogeneity of soil resources, leading to so-called islands of fertility around trees and shrubs (Figure 1) [11]. These islands of fertility result in discontinuous distribution of both water and nutrients.

These constraints on productivity reduce the biomass of the soil microbial community in semiarid systems when compared to that of temperate or tropical ecosystems. Actinomycetes are one of the few groups of microorganisms which are actually more common in xeric environments as compared to more mesic locations. This is a group of autochtonous and filamentous bacteria which is adapted to low soil water potentials. Ants can also be really abundant and diverse in desert soils, and their mounds can sometimes be detected from aerial photographs (Peter D Stahl, *pers. comm.*).

The aforesaid environmental heterogeneity in above- and below-ground organisms results in patches with no vegetation cover in desert ecosystems [3]. However, these patches free of vegetation do contain autotrophic organisms such as cyanobacteria, lichens, and mosses which, together with fungi and bacteria form soil microbial crusts [12]. These crusts can occupy up to 70% of intercanopy space and are found in all the different semiarid regions around the world [13].

Another factor regulating the density and composition of soil microbial populations and communities are biotic interactions. Competition is probably the most important interaction. Following pulses of precipitation, microbial activity starts and competition for limited resources is strongest. During dry periods, competition is not that important because microbial activity is inhibited. Symbiosis are also very important in these environments. Soil microbial crusts and N_2 fixing bacteria living in plant roots are examples of this.

Figure 1. Islands of fertility developed around *Larrea tridentata* stems in Death Valley, CA.

However, there is still an enormous gap of knowledge on the identity and abundance of soil microorganisms. Future research should include the development of new tools in the field of molecular biology and a more exhaustive classification of organisms in functional types (Brussard *et al*, 1997).

SOIL RESPIRATION

Cable and Huxman[14], analysing $\delta^{13}C$ of respiratory CO_2 efflux, found that the relative contribution of soil microbial crusts to CO_2 efflux differed with precipitation pulse sizes. In the control treatment (no water addition), the contribution of crusts was slightly over 50 %. After a small pulse event (2mm), this percentage raised to over 80%, but after a large pulse event (25.4 mm), it dropped to nearly 0%. Rainfall events in the three warm deserts of North America (Mojave, Sonoran and Chihuahuan) are dominated by pulse events smaller than 2 mm. Therefore, in these warm semiarid systems, crusts are potentially the sole contributors to ecosystem carbon cycling following the majority of rain events. Therefore, a change in precipitation regimes, as predicted by climate models, in a pulse driven ecosystem may alter respiratory responses from the soil as a whole [15]. Not only the total amount of precipitation is expected to increase, but also (and maybe more important) the frequency of different sized pulses [16]. This indicates that future studies should monitor how changing annual precipitation and pulse size affects soil respiration, and especially soil microbial crusts respiration.

CARBON AND NITROGEN DYNAMICS

A principal consequence of the stochastic nature of water inputs in arid and semiarid ecosystems is that surface soils experience periods of drying followed by relatively rapid rewetting. These wet-dry cycles affect all aspects of carbon and nutrient turnover, including C and N mineralization, microbial biomass, gaseous losses, denitrification and ammonia volatilisation (8 and references therein).

Wet-dry cycles initially stimulate C and net N mineralization, diminish microbial biomass during drying but stimulate microbial growth after wetting, and the wet-dry cycle itself results in higher net N and C mineralization when in systems driven by water pulses compared to continuously moist soils [17, 18].

Under dry conditions, a part of the microbial population dies when the soil water potential drops below the “critical cell water potential”, and they are readily decomposed by surviving organisms when the soil is rewetted [8].

C and N mineralization in response to a pulse are influenced by i) the magnitude of the pulse; ii) the duration and number of wet-dry cycles (with more cycles, increased C and N mineralization) [17]; iii) the time between each cycle (as time increases, a bigger portion of microbial populations will be killed) and iv) the size of the pool of soil labile C and N [19].

An important point to understand pulse effects on nutrient dynamics is the asynchrony of resource availability. Cryptobiotic organisms at the soil surface can respond to small pulses that only wet the top soil layer, therefore increasing nutrient availability. Plants, however, may not be activated by such small rainfall events and, consequently, may not able to uptake this available resource [8, 14]. However, such responses do not seem to be universal as [20] showed that *Artemisia tridentata* and *Agropyron desertorum* were capable of utilizing nitrogen pulses following small summer rainfall events (5 mm) even during the most stressful period of the summer. These contradicting results highlight the necessity for further understanding of nutrient dynamics following small pulses of precipitation.

According to [8], in water-limited ecosystems, N mineralization and immobilization by soil microbes is mainly determined by: i) the ratio of C/N in organic substrates consumed by the microbial community, ii) the N-use efficiency (NUE) and iii) the growth efficiency (GE) of the microbial community (Figure 2).

The C/N ratio determines which group of organism will be more abundant: bacteria will dominate at higher C/N ratios, whereas fungi will be more common at low C/N ratios. This ratio also influences the N mineralization: N immobilization ratio, which increases at higher C/N ratios, and can explain the pulse of mineralization commonly observed after wetting of semiarid soils [8].

Fungal NUE (the amount of N necessary to produce one unit of microbial biomass C) is bigger than bacterial NUE. This, together with higher tolerance of fungi to desiccation, may shift microbial community in the dry season towards higher fungi densities, therefore slowing down mineralization rates [8].

GE is the amount of organic C necessary to produce one unit of microbial biomass C. High GE leads to N immobilization and low GE to N mineralization because the greater the GE, the greater the N-demand.

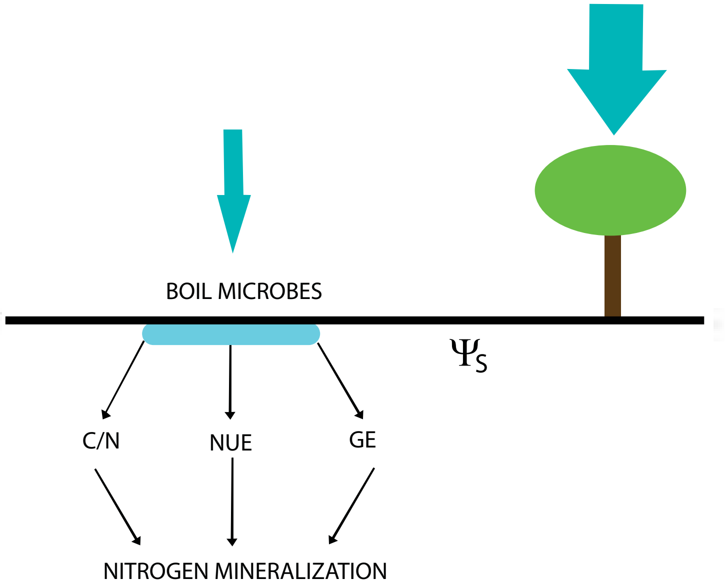

Figure 2. Conceptual diagram indicating the effects of pulses of different sizes on soil microbiological activity. Large pulses will be mainly used by trees whereas microbes will take higher benefit from smaller pulses. Soil water potential, Ψs, represents the soil water conditions previous to the pulse. C/N, NUE and GE are the intrinsic properties of the microbial community that will determine the rate of nitrogen mineralization after a pulse. See text for further details.

Nitrogen fixed by the soil microbial crust can be the dominant source of N, especially in regions where rainfall and anthropogenic inputs of N are low [21]. In an experiment in Canyonlands National Park (Utah, USA), Belnap (2002) showed that differences in N fixation among soil microbial crusts seem to be species-specific and vary with environmental conditions. Moisture availability and temperature are the main environmental factors controlling nitrogenase activity. Nitrogen fixation is smaller following a pulse after extended dry periods, than under short time periods, and temperature needs to be between 1 and 26ºC.

DECOMPOSITION

Unfortunately, no studies were found studying the short term effects of pulses on decomposition rates. Therefore, this section is focused on the long-term effects of drought in semiarid ecosystems

Decomposition is the breakdown of organic matter to CO_2, water and nutrients. It is controlled by the physical environment (moisture, temperature, pH, O_2 concentration), by the substrate quantity and quality and by the microbial community. According to [22], semiarid forests have the slowest decomposition rates in the world, together with subarctic and subalpine forests. In that same study, when compared to tropical forests, mean residence time (an indicator of decomposition rate calculated as biomass of forest floor divided by biomass of annual litterfall) of semiarid forests was two orders of magnitude higher than tropical forests. An artifact of this study, however, is that biomass of annual litterfall was calculated only from aboveground components, and this could lead to big overestimates of the residence time.

Soil organic matter (SOM) decomposition is activated when diffusion is no longer restricted after a pulse event. Wet-dry cycles may cause the disruption of soil aggregates, exposing physically protected organic matter and increasing the accessibility of substrate that can be rapidly mineralised [23]. One of the more uncertain aspects of nutrient cycling in semiarid ecosystems is the extent to which decomposition is controlled by water availability [24]. Lack of water has direct and indirect effects on this low decomposition rates. Leaching by water is the first process of decomposition. Lack of water is probably directly limiting this step. Because water is also limiting soil organisms density (see *Distribution* and *abundance* of soil biota), it is also affecting indirectly the other two steps of decomposition: fragmentantion by soil animals and chemical alteration by microbes. Another reason why drought is limiting decomposition is because the soil solution is the media where many important reactions take place.

Kemp *et al.* (2003) conducted a 3-year field study of rainfall to determine the impact of summer (June – September) drought on decomposition of leaf and root litter of two shrub species (*Larrea tridentata* and *Prosopis glandulosa*) in the northern Chihuahuan Desert (New Mexico, U.S.A.). In both species, leaf litter decayed at a faster rate and was less affected by drought than root litter. Drought had no influence on the rates of decomposition of leaves of either species during the first 18 months, but caused decay rates to decline by about 25% during the latter half of the study. Drought decreased decay of root litter in both species by about 25% throughout the 3 years. The main conclusion of their study is that relatively large changes in precipitation produce comparatively small changes in rates of decay of both leaf and root litter.

Increased drought also reduces enzymatic activity. By reducing the soil volumetric water content (VWC) in 10 %, [25] found a decreased urease activity by 10–67%, protease activity by 15–66% and β-glucosidase activity by 10-80%, depending on annual period and soil depth. In the same experiment, when (VWC) decreased by 21%, urease activity was reduced by 42–60%, protease activity by 35–45%, β-glucosidase activity by 35–83% and acid phosphatase activity by 31–40%. They also found that the activities of the enzymes involved in the nitrogen cycle, protease and urease, were the most affected by drought.

CLIMATE CHANGE AND INVASIVE SPECIES

Anthropogenic emissions of greenhouse gases have increased exponentially in the last few decades [26]. CO_2 is considered as the most important greenhouse gas because of its high concentration in the atmosphere (380 ppm). These increases in greenhouse gas emissions are expected to raise the Earth's surface mean temperature by 1.4ºC to 5.8ºC during this century [26]. Such warming will likely alter patterns of global air circulation and hydrologic cycling that will change global and regional precipitation regimes [26]. How will the hydrologic cycle be modified is still not very well understood. For example, a Canadian Centre for Climate Modelling and Analysis model (GCM1) predicts reduction in summer and winter precipitation in the Southeast and Great Plains regions of the United States by 2095, whereas a model developed by the Hadley Centre for Climate Prediction and Research (HadCM2) predicts increased precipitations throughout most of the United States, and particularly the Southwest, over the same time period. Both models coincide in that tropospheric warming will increase evaporation rates and thus increases the severity of drought despite potential increases in precipitation in some regions. Both models also agree in that the intensity of precipitation events and the frequency of extreme events, which have already increased across the globe, are predicted to increase further [16].

To sum up, we can expect three major impacts of climate change on microbial communities and processes: 1) Increases in CO2 concentrations; 2) Increases in temperatures and 3) Changes in precipitation patterns, including changes in the seasonality of precipitation and in the intensity of extreme events. In response to these climate shifts, plant communities are expected to be modified [27], and the introduction of new invasive species is expected to exacerbate [28]. Figure 3 summarizes these effects and their impact on soil microbial communities.

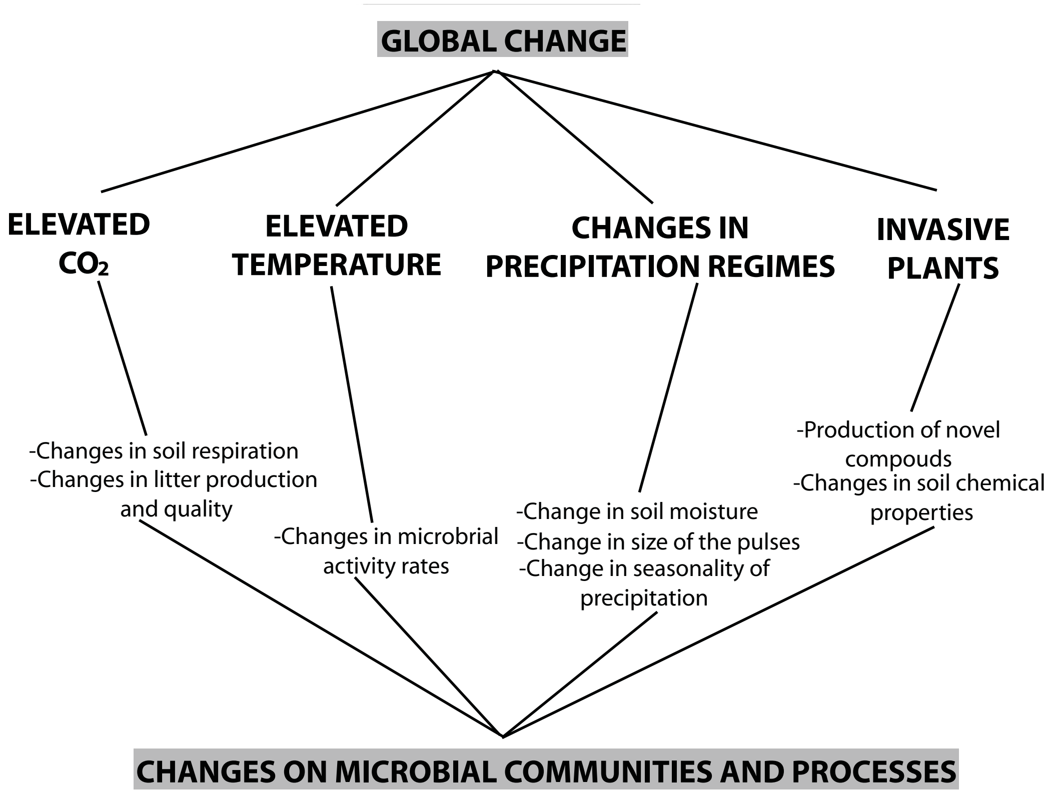

Figure 3. Summarized effects of climate change and invasive species on soil microbial processes.

EFFECTS OF ELEVATED CO_2

[29] showed that soil respiration increased under high CO_2 concentrations in open top chambers, with bigger increases on dry than on wet summers in the semi-arid stepped of Colorado (USA). One of the possible artefacts with open top chamber experiments or FACE technology is that there is only high and control CO_2 concentrations, and all the models are based on a straight line between these two points. These artefacts are likely to be solved soon because 2nd generation FACE experiments include a gradient of CO_2 concentration and will allow for more detailed studies of these mechanisms. This technology is still in experimental phase, but they will be able to provide sound data in the next few years.

With increasing CO_2 concentration, plant tissue C/N ratio decreases. Given that decomposition is highly dependent on the substrate, it has been hypothesized that litter should also increase its C/N ratio, and therefore diminish litter quality, which should have an impact on decomposition [30]. However, available data have not supported this hypothesis in mesic ecosystems, and the little data available for desert or semi-arid ecosystems points towards the same direction [1, 31]. For the Mojave desert, [1] found that in situ litter decomposition and litter-mediated ecosystem N and C cycling, likely will not change substantially as a direct result of the continuing rise in atmospheric CO_2 levels – even though litter chemical quality likely will decrease. These results are interesting because they show how decomposition is not as closely linked to substrate quality as originally thought, and opens new areas of research for the mechanisms driving decomposition. Weatherly *et al*, (2003) also suggest that interannual climate variability (especially differences in annual rainfall) – and the potential changes in climate caused by human activities (e.g. increases in relatively wet El Niño years) – may lead to large changes in litter production and litter species.

EFFECTS OF ELEVATED TEMPERATURES

Optimum temperatures vary between and within different groups of organisms, but most soil microorganisms show optimum growth conditions between 25-45ºC. At higher temperatures, proteins suffer denaturalisation, and microbes need certain adaptations to deal with this (an example would be thermophilic bacteria in Yellowstone) (for studies on the limits to life in desert ecosystems see [32, 33]. At lower temperatures, microbial activity is slowed down or inhibited because of lack of energy to perform reactions and because of freezing and death, although some studies have shown ecosystem respiration at –50ºC in boreal forests [34]. Low (<1ºC) and high (>26ºC) inhibit nitrogen fixation by inhibiting nitrogenase activity [21].

After a pulse event, temperatures are generally refreshed. This could be important especially in warm deserts where surface soil temperature can reach 60º C (V Resco, *pers. obs.)*. Therefore, ameliorated temperatures are likely to be one of the reasons for the bursts in microbial activity following pulses of precipitation. Therefore, increased temperatures in warm semiarid forest has the potential to inhibit microbial communities and their processes.

Traditionally, semiarid ecosystems have been assumed to be water driven, whereas in regions with more precipitation like temperate or subalpine ecosystems, have been assumed to be temperature and nutrients driven [2]. As temperature increases, it is likely that they will become more and more limited by this factor, and, if temperature increases as predicted in the worst case scenario by [26], that is, 5.8ºC, it is possible that these systems will be temperature and precipitation driven.

To our knowledge, there is no study which directly addresses these in questions in arid environments, as the effects of temperature are more studied in arctic and alpine environments.

EFFECTS OF CHANGING PRECIPITATION REGIMES

There are three main effects of changing precipitation regimes on microbial communities. The first and more obvious is the change in the amount of soil moisture. The second is the change in the size of the pulses. For example, the amount of small pulses could diminish and that of big pulses increase. The third includes changes in the seasonality of precipitation, that is, changing from a winter precipitation system to a bimodal or summer precipitation system.

As summer rainfall increases, soil lichen cover has been reported to decline at global scale [35]. [35] showed that under field conditions of high air temperatures and frequent, small precipitation events, crust organisms appear unable to produce protective pigments in response to radiation stress, as they likely dried more quickly than when they received larger, less frequent events. Reduced activity time likely resulted in less carbon available to produce or repair chlorophyll *a* and/or protective pigments, and partly explained the abovementioned lichen decline. Increasing annual rainfall should be more beneficial to bacteria (except actinomycetes) than to fungi.

A comprehensive analysis of the different effects that large pulses vs. small pulses of precipitation could have on microbial communities and on the effects of changing seasonality yet remains to be done. Species and functional traits composition will probably be modified, and this may change microbial processes.

EFFECTS OF INVASIVE SPECIES

Invasive plant species, by affecting plant communities and substrate for decomposition, have the potential to impact soil microbial community and soil properties [36]. Invasive plant species can alter native microbial populations in two different ways: i) producing new antimicrobial compounds novel to that populations, and ii) altering the soil chemical properties.

It has been proposed that some invaders have certain root exudates that are relatively ineffective against their natural competitors in their original distribution range because the latter are adapted to these biochemical compounds. When this invasive plant species is introduced to a new environment, the new neighbors this species encounters are not adapted to tolerate these compounds. The invader then benefits as mediator for new plant-soil microbial interactions [37]. There are reasons however to think that certain microbe populations may evolve to tolerate this new soil environment created by this novel invader and that this may lead to their proliferation. The effects of novel biochemical weapons on soil biota may also drive invasions. The combination of novel plants and microbial species that have not shared evolutionary paths may cause also changes in microbial community composition. The extent and genereality of this phenomenon, however, still remain uncertain.

The most direct and known effect of invasive plant species on soil biota lies on changes in litter quality, that may drive changes in the biogeochemistry of the system [38]. It has been widely documented how different microbial communities are associated with different plant species ([39], [37, 40, 41]. Consequently, new invasive plants will produce species-specific effects on soil microbe populations.

These changes may result from alterations in the patterns of species dominance within the plant community, because the effects of a given species on ecosystem processes are modulated by its relative importance in the community [42]. The effect that changes in soil biogeochemistry driven by plant invasions may have on global biogeochemistry yet remains to be explored.

Interesting positive feedbacks between invasive plants and changes in soil biota have been documented by [43]. Many ecosystems are becoming more susceptible to invasions by exotic plants because they contain an increasing array of potential mutualistic partners such as mycorrhyzal fungi with wide host ranges,or rhizobia strailns with infectivity across genera.

CONCLUSIONS

The duration and size of pulse events and dry periods are the most important factors affecting the distribution and abundance of soil biota in semiarid forests. Consequently, they also influence C and N dynamics, decomposition and soil respiration. These relationships are expected to be modified under increasing CO_2 concentrations and temperature, and changing precipitation regime. The mechanisms driving these processes are still largely unknown and there are big uncertainties about their predicted responses to climate change. Future research needs include factorial and well-replicated experiments on the dynamics following different sizes of precipitation with different temperature and CO_2 concentrations, for semiarid forest ecosystems.

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Chapter 3

THE ROLE OF ATMOSPHERIC N DEPOSITION IN SOIL ACIDIFICATION IN FOREST ECOSYSTEMS

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ABSTRACT

The emissions of NO_x and NH_3 into the atmosphere are on the rise, and the emitted N compounds are distributed globally, causing concerns over possible effects on human health and the environment. The emission of N occurs primarily from agricultural activities and fossil-fuel combustion (e.g., automobile and industrial boilers). Atmospheric N deposition has become an important factor affecting forest health and sustainability in recent decades, partly as a result of decreasing S emissions. Nitrogen compounds that fall onto soil and water bodies with precipitation and dry deposition can cause damage to ecological systems. Chronic excessive N input can lead to base cation depletion, nutrient imbalances, eutrophication, soil acidification, and forest dieback. Leaching losses of NO_3^- gradually decrease the acid buffering capacity of forest soils. Moreover, releases of Al and Mn induced by soil acidification cause toxicity to trees. Biological processes play a crucial role in soil acidification, as N compounds originated from atmospheric deposition undergo nutrient cycling processes. However, the effects of N transformation on soil acidification in forest ecosystems are often overlooked. Thus, an improved understanding of the impact of atmospheric N deposition on N cycling processes is needed to better predict the responses of forest ecosystems to such depositions. In this paper, we explore the linkage between N cycling and soil acidification in forest ecosystems, and evaluate the role of N cycling and atmospheric N deposition on soil acidification in forest ecosystems by discussing: 1) the N cycle and its effect on soil acidification in forest ecosystems, 2) the effect of N deposition on forest soils and trees, in terms of base cation depletion, soil acidification, and aluminum

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toxicity, 3) leaching losses of N from forest soils, and 4) critical loads of atmospheric N deposition in forest ecosystems.

Keywords: Acidification, Aluminum, Buffer Capacity, Ca/Al Ratio, Critical Load, Mineralization, Nitrification, Nitrate, N Saturation, Nitrogen Leaching

1. INTRODUCTION

The influence of elevated atmospheric deposition of N and S compounds on forest ecosystems has received increased attention since the early 1980s, as a result of concern over the state of forests (Galloway et al., 1984; Galloway, 1995). The acidifying effects of atmospheric deposition of sulphuric compounds in relation to the release of Al and loss of base cations such as Ca in the soil caused most of the observed forest decline in central Europe and northeastern United States in the 1980s (Shortle and Smith, 1988; Jandl et al., 2004). Input-output budgets derived from intensively monitored ecosystems in Europe indicated a quantitative relationship between atmospheric acidic N and S inputs and the release of Al, based on data obtained before 1980 (Erisman and de Vries, 2000). The acidification process also leads to lower levels of soil base cation concentrations.

High levels of soluble Al are harmful to many plant species and soil-dwelling organisms, as they are adapted to a specific level of acidity. Thus, soil acidification may lead to the disappearance of some species and their subsequent replacement by other species. For example, Graveland et al. (1994) showed that poor reproduction in forest passerines was caused by the decline of snail abundance in acidified soils. The general tendency is for species diversity to decline with rising acidity (Gorham, 1998; SwEPA, 2000).

In earlier studies, pollutants of primary interest were sulfur dioxide (SO_2) and its oxidation products. However, atmospheric inputs of N as a cause of forest decline have gained increasing attention during the last decade. This is coupled with a large decrease in S emission since the introduction of the first Sulphur Protocol in 1985, in which signatory states pledged a 30% reduction in S emissions by 1993 as compared with the 1980 level. The second Sulphur Protocol, which was established in 1994, required that S emissions be halved from the 1980 levels by the year 2000 (Vuorenmaa, 2004). In contrast, emissions of NO_x and NH_3 have hardly changed, and the potential effects of N deposition on forests may be greater than that of S deposition (Erisman and de Vries, 2000). Oxides of N such as NO_x emitted from combustion sources could also make an important contribution to ecosystem acidification. Key international instruments for emission abatement strategies are the multi-effect, multi-pollutant protocol signed in Gothenburg in 1999, and the European Commission’s national emission ceilings directive in 1999, although the first NO_x Protocol was signed in 1988 (Vuorenmaa, 2004). At present, the N to S ratio in atmospheric deposition is generally greater than one. For example, Erisman and de Vries (2000), based on compiled data for bulk precipitation and throughfall from more than 150 plots, showed that atmospheric deposition of N exceeded that of S in Western and Central Europe, but the relative contribution of NH_4^+ and NO_3^- in the overall N deposition varied by location. Moreover, the transformation of nitrogen oxides to acidic end products is closely linked to the atmospheric processes producing other primary pollutants such as ozone and peroxyacetylnitrate (Irwin and Williams, 1988). However until comparatively recently, N deposition onto large water bodies has been relatively poorly quantified, so that the extent of the impact of N deposition on large water bodies is still not well known.

Nitrogen is usually a limiting nutrient for terrestrial vegetation, but where the input of inorganic N is excessive, the capacity of biota to assimilate N can be exceeded by the rate of input. One of the consequences of atmospheric acidic deposition of N is that forest ecosystems, which have historically been thought of as N-limited, are becoming N-saturated (Aber et al., 1989). Although forest productivity may initially increase due to the high deposition levels, N saturation in forest ecosystems will eventually decrease forest health through soil acidification. High rates of atmospheric N deposition can also increase water stress (Drohan et al., 2002), nutrient leaching (Kolb and McCormick, 1993), and unbalanced tree nutrition (Spoelstra, 2004), while decrease forest tolerance to stress, species diversity of the ground vegetation, and tree growth. Because soils have natural acid-buffering capacity, the acidification of even very sensitive soils is a slow process that may take many decades before changes become measurable. Thus, the question of long-term effects of acidic deposition on forest ecosystems is important especially in the development of public policies (Bloom and Grigal, 1985).

Biological processes play a crucial role in soil acidification, as the transformation of N (NH_4^+ or NO_3^-) originating from atmospheric N deposition can cause acidification. However, the impact of N transformation on soil acidification in forest ecosystems is often overlooked. Better predictions of ecosystem responses to atmospheric N and S deposition will require an improved understanding of these biogeochemical processes that include biological uptake, return through litterfall, sorption/desorption processes, cation leaching and precipitation (Matson et al., 2002).

This paper will explore the linkage between N cycling and soil acidification in forest ecosystems. Our discussion on the role of N cycling and the effect of atmospheric N deposition on soil acidification in forest ecosystems will be focused on the following four topics: 1) the N cycling in relation to soil acidification in forest ecosystems, 2) the effects of N deposition on forest soils and trees in terms of base cation depletion and Al toxicity, 3) leaching losses of N from forest soils, and 4) critical loads of atmospheric acidic N deposition in forest ecosystems.

2. ATMOSPHERIC N DEPOSITION

2.1. Emissions of NO_x and NH_3

In the atmosphere, $N_{2,}$, an inert gas, makes up about 78% of the dry troposphere (up to 10 ~ 20 km above the earth’s surface). Nevertheless, anthropogenic N compounds in the atmosphere are included as one of the four major classes of air pollutants, together with S compounds, volatile and semi-volatile organic compounds, and toxic metals, all of them may cause detrimental effects to human health and the surrounding environment (Krupa, 2003). Atmospheric N species occur as gases and particles, and include oxides of N, ammonia, ammonium, peroxyacyl nitrates (PANs), nitric acid, and other inorganic and organic nitrates. The principal precursor of atmospheric N deposition is primarily N oxides (NO_x), but concentrations of other compounds such as ammonia (NH_3) also significantly influence the potential acidity of the precipitation.

Among all N species, NH_3, NO_x and N_2O account for approximately 55%, 40% and 5%, respectively, of the total anthropogenic N emission. Krupa (2003) provided a good review of the contribution of the different N species to total anthropogenic N emission. With regard to sources of N emissions, agriculture is by far the largest at 50%, fossil fuel combustion from stationary and mobile sources at 30%, and biomass burning contributes another 10% to the total emission (Irwin and Williams, 1988).

Nitrogen oxides (NO and NO_2) play an important role in atmospheric deposition of N as a precursor of acidity. High temperature combustion of fossil fuel constitutes a major anthropogenic source for NO_x. The NO is formed both from N that is present in the fuel and from the oxidation of N_2 in atmosphere. Biomass burning is also a major source of NO, and other processes such as lightning, microbial activity in soils, and ammonia oxidation contribute to the emission of NO_x. Anthropogenic emissions arising from fossil fuel combustion occurred mainly from Europe and North America, reflecting past economic activities in those regions that lead to increased fuel combustions (Irwin and Williams, 1988). Although ammonia is one of the major acid neutralizing compounds in the atmosphere, until recently, its emission source had been poorly studied, as compared to NO_x. In Europe, emissions of reduced N species (NH_3) from agriculture were characterized by marked increases in the mid twentieth century, peaking in the late 1980s (Vuorenmaa, 2004). The major sources of NH_3 emission are volatilization from animal wastes and synthetic fertilizers, biomass burning such as forest fires, N losses from soils under native vegetation and agricultural crops, emissions from human excreta, and fossil fuel combustion (Oliver et al., 1998; Krupa, 2003). The estimated emissions of anthropogenic and natural sources for NO_x and NH_3 are presented in Table 1.

For NO_x emissions, the estimated global anthropogenic sources identified include fossil fuel combustion (68%), of which the major sources are transportation vehicles and power plants, and biomass burning (25%). Natural sources contribute approximately 19 million ton N year^{-1} mainly from lightning (63%) and through soil processes (28%) (Table 1). In addition, Derwent et al. (2004) estimated that NO_x emissions for the 1990s occurred mainly from industrial processes (31.7), biomass burning (7.1), soil processes (5.6), lightning (5.0) and aircraft (0.5 Tg N year^{-1}), a distribution similar to that predicted by Oliver et al. (1998).

For NH_3, the estimated global emission in 1990 was approximately 54 million ton N year^{-1}. The major sources identified include excreta from domestic and wild animals, use of synthetic N fertilizers, natural emission from oceans, and biomass burning (Table 1). Similarly, the major sources of NH_3 emission for the 1990s reported by Derwent et al. (2004) were industrial processes (39.3), oceans (8.2), biomass burning (3.5) and soil (2.4 Tg year^{-1}). In Europe, total emissions of NO_x and NH_3 in 2000 decreased by approximately 25 and 18%, respectively, as compared to 1990.

2.2. Transformations of N Compounds in the Atmosphere

Transformations of NO_x and NH_3 in the atmosphere are outlined in Figure 1. Nitrogen dioxide (NO_2) competes with SO_2 for OH radicals, and the reaction is the major route for the formation of nitric acid in the atmosphere (Figure 1). The rate constant for the [NO_2 + OH] reaction is about an order of magnitude higher than that for the [SO_2 + OH] reaction. Thus, the reaction of hydroxyl ion (OH) with NO_2 is favored in the atmosphere, producing nitric acid. The deposition velocity of nitric acid is largely controlled by the prevailing boundary layer turbulence, and is thus strictly a function of atmospheric conditions. The reaction of H_2SO_4 with NH_3 is generally considered to be very fast, producing ammonium sulfate aerosol (Figure 1).

In contrast to the sulphur system, there is no significant aqueous transformation pathway for nitric acid production (Hoffmann and Jacob, 1984). Wet removal of N species generally involves scavenging of both gaseous species and particulate aerosols (Irwin and Williams, 1988). Direct removal of nitric acid from the atmosphere by rainfall can be estimated using a wash-out coefficient, as was reviewed in Garland (1978). In addition, the wet removal can be assessed using a scavenging ratio, the ratio of N concentration in rain to that in air, which typically ranges between 10^4 and 10^6.

Table 1. The major global anthropogenic and natural sources of emissions of NO_x and NH_3 in 1990 (modified from Oliver et al., 1998)

Source		Emission of NO_x		Emission of NH_3	
		10^{12} g N $year^{-1}$	%	10^{12} g N $year^{-1}$	%
Anthropogenic sources	Fossil fuel combustion (surface)	21.3	42.3	0.1	0.2
	Aircraft	0.6	1.2	-1)	-
	Industrial processes	1.5	3.0	0.2	0.4
	Animal excreta	-	-	21.6	40.2
	Synthetic fertilizer use	-	-	9.0	16.8
	Crop decomposition	-	-	3.6	6.7
	Biomass burning	7.7	15.3	5.9	11.0
	Human excreta	-	-	2.6	4.8
	Subtotal	31.1	61.7	43.0	80.1
Natural sources	Soil microbial production	5.5	10.9	2.4	4.5
	Oceans	-	-	8.2	15.3
	Lightning	12.2	24.2	-	-
	Excreta of wild animals	-	-	0.1	0.2
	Atmospheric NH_3 oxidation to NO_x	0.9	1.8	-	-
	Stratospheric destruction of N_2O	0.7	1.4	-	-
	Subtotal	19.3	38.3	10.7	19.9
	Total	50.4	100.0	53.7	100.0

[1] Indicates no data available or not identified as a source.

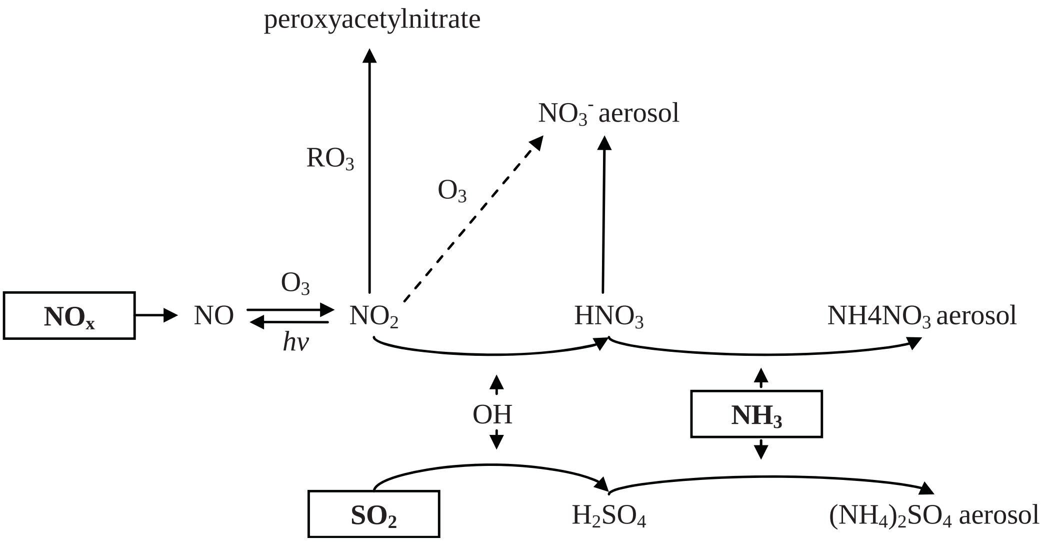

Figure 1. Major forms and pathways for SO_2, NO_x and NH_3 transformations in the atmosphere (source: Irwin and Williams, 1988).

In general, the water solubility of NO and NO_2 is very low, and thus it is regarded that a direct removal of these gases by rain is negligible. However, nitric acid is highly soluble in water, and thus can be rapidly scavenged by rain. The wet removal of nitrate aerosol arises from the impaction of the particulates by a scavenging process called nucleation where the particles act as a cloud condensation nuclei. But, the scavenging process varies depending on the particle size of nitrate aerosol, rain drop size and rainfall intensity, with a typical scavenging ratio of 5×10^5 for nitrate aerosol (Irwin and Williams, 1988).

Ammonia (NH_3) reacts readily with acidic substances such as sulfuric acid, nitric acid, nitrous acid, or hydrochloric acid to form ammonium salts that occur predominantly in the fine particle size (< 2.5 μm) fraction. The formation of fine particulate NH_4^+ salts is a very effective mechanism that removes gaseous NH_3 from the atmosphere. This conversion is most effective in the lowest (below ~ 100 m) layer of the atmosphere, and is generally known to occur much faster during the daytime than at night (Erisman et al., 1988). Since NH_3 is quickly transformed to NH_4^+ or subjected to dry deposition, high concentrations are found only near the surface or emission sources (Ferm, 1998; Krupa, 2003). Horizontally, NH_3 concentrations decrease as distance from the source increases. For example, Asman et al. (1989) measured NH_3 concentrations in an area with a high emission density in a moorland, and observed a 70% decrease in NH_3 concentration at 4 km from the boundary of the emission area.

Fine particles are generally transferred to the surfaces by Brownian motion, and their deposition is not significantly affected by gravity. Thus, particulates of ammonium sulfate or ammonium nitrate have prolonged atmospheric residence time. However, the vertical distribution of NH_4^+ concentration is much more uniform as compared to that of NH_3. In contrast to NH_3 (high concentrations close to surface), NH_4^+ concentrations were found to be higher than NH_3 at heights above 200 m. The horizontal distribution of NH_4^+ is little affected by its closeness to NH_3 sources (Krupa, 2003).

2.3. Atmospheric Deposition of N

The products of various chemical and physical reactions involving N in the atmosphere are eventually deposited back to the terrestrial ecosystems. In general, three major pathways exist whereby atmospheric acidic N species, which may be present as gases or aerosols, are transported to the ground: 1) by hydrometeor (any product of deposition of atmospheric water vapor, whether formed in the free atmosphere or at the earth's surface), termed wet deposition; 2) by direct deposition, a process known as dry deposition; or 3) by occult deposition, a process in which N compounds are captured by surfaces by the impaction of cloud or fog droplets on to vegetation. The term atmospheric acidic deposition is used to include all these processes (Irwin and Williams, 1988), while wet and dry depositions are usually distinguished. In this case, wet deposition covers the deposition of dissolved and particulate substances contained in rain or snow, whereas dry deposition includes the deposition of particles and gases such as HNO_3, NH_3, and SO_2 to the receptor surface in the absence of rain and snow. In forest ecosystems, approximately 50% of the deposition of NO_3^-, SO_4^{2-}, and H^+ are known to occur as dry deposition (Schnoor, 1996).

Wet Deposition

Wet deposition occurs when pollutants fall onto ground or sea by rainfall, snowfall, or hail. Wet deposition to the earth's surface is directly proportional to the concentration of pollutants in the rain, snow, or ice. Thus, the wet deposition flux can be expressed by (Schnoor, 1996):

$$F_{wet} = IC_w \tag{1}$$

Where F_{wet} is the aerial wet deposition flux (μg cm^{-2} s^{-1}), I is the precipitation rate (cm s^{-1} as liquid H_2O), and C_w is the concentration (μg cm^{-3}) of the pollutant in the precipitation.

The concentrations of hydrogen ion and ammonium are usually in approximate balance with non-marine sulfate and nitrate, and the concentrations of these four major ions are usually highly correlated. Concentrations of the gaseous and aerosol precursors of these species all tend to be high in polluted air masses and uniformly low in clean air (Irwin and Williams, 1988). In northeastern United States, maximum contributions of sulfuric and nitric acid deposition to total acidic deposition have been reported to be approximately 73% and 31%, respectively, in summer, and 59% and 61%, respectively, in winter (Galloway and Liken, 1981). Proportions of 70% and 30% for sulfuric and nitric acid contributions, respectively, to acidic deposition have also been reported in the United Kingdom (Fowler et al., 1982).

Ammonia and the derived NH_4^+ are removed from the atmosphere both by dry and wet deposition. Wet deposition occurs by rainout (in-cloud processes) and below cloud scavenging (washout processes). Ammonium salts such as $(NH_4)_2SO_4$ are hydroscopic, and act as cloud condensation nuclei. Wet deposition is more important in regions with low emissions, even though the actual situation is affected by local variability in precipitation type and intensity (Irwin and Williams, 1988).

Dry Deposition

Dry deposition occurs by diffusion of NH_3 and Brownian motion of particulates containing NH_4^+, and to a much lesser extent, by sedimentation of coarse particles (< 2.5 μm). It is important to note that a major portion of NH_4^+ occurs in the fine particle size (Finlayson-Pitt and Pitts, 1999). In the absence of rainfall, dry deposition can take place in two forms: aerosol and particle deposition, and gaseous deposition. The velocity of dry deposition can be expressed as follows (Schnoor, 1996):

$$V_d = (r_a + r_b + r_c)^{-1} \tag{2}$$

Where V_d the velocity (cm s^{-1}) of dry deposition, r_a is the aerodynamic resistance, r_b is the boundary layer resistance, and r_c is the resistance at the surface of receptor.

The dry deposition of gases and particles is largely governed by the turbulence structure of the boundary layer and receptor properties as described in equation (2), except for large particles (typically with 30 ~ 100 μm diameter or greater), whose sedimentation velocity exceeds turbulent velocities. As most interest concerns gases and S- and N-containing particles (typically of diameter < 1 μm) formed as a result of photochemical and other reactions, it is difficult to extrapolate results obtained using surrogate surfaces to natural ones (Hicks, 1986; Irwin and Williams, 1988). Therefore, fluxes of dry deposition are usually calculated as the product of near-surface concentration of N-containing compounds, and the deposition velocity. Initially, these methods assumed constant deposition velocities, but the seasonal variability of deposition velocity and receptor surface condition have also been considered (Fowler, 1984). In contrast to wet deposition, dry deposition is more important in regions with high rates of N emissions (Irwin and Williams, 1988).

Occult Deposition

Wind-blown cloud and fog droplets may be intercepted directly by vegetation. The concentrations of acidic N species in such droplets can be much higher than in rain drops, where dilution has taken place. Although the importance of occult deposition has long been recognized in hydrological work, it is only recently that attempts have been made to estimate its contribution to acidic N deposition. Theoretical estimates of its magnitude suggest that it is an important transfer mechanism in localized areas, such as hill tops that are covered in cloud during most of the year, but of only minor significance to the N budget on a wider scale (Irwin and Williams, 1988).

A major question in precipitation chemistry being studied in recent years has been whether a reduction or an increase in atmospheric acidic emissions will lead to a proportional change in the deposition of pollutants such as N compounds. What goes up does, of course, comes down, and when averaged over a long enough time and large enough area, the overall relationship between rates of emission and deposition must be approximately proportional. It seems likely that in the N system, the relationship between emissions and deposition will be approximately proportional, although firm conclusions must await further investigations (Irwin and Williams, 1988).

3. NITROGEN CYCLING AND ITS MASS BALANCE

Most of the N in terrestrial ecosystems is present as fixed N in the earth's crust in rocks and sediments. The second largest pool of N is N_2 (gas) in the atmosphere. A relatively small amount of N in the soil is available for plants either in oxidized or reduced form. The biosphere in its original condition is adapted to a low availability of N, and more than 90% of plant N uptake is provided by an internal cycling within biosphere (Erisman and de Vries, 2000). One example of internal cycling is N translocation from leaves to woody tissues that occur before leaf senescence.

3.1. Nitrogen Transformations in the Soil

The N cycle is defined as the sequence of biochemical changes, where N is utilized by living organisms, transformed upon decomposition of the organisms, and converted ultimately to its original oxidized state (Soil Science Society of America, 1997). Nitrogen transformation processes are essential for the sustainability of long-lived forest ecosystems. Nitrogen deposition and fixation throughout the biosphere restore losses of N from the soil N cycle (Offord, 1999).

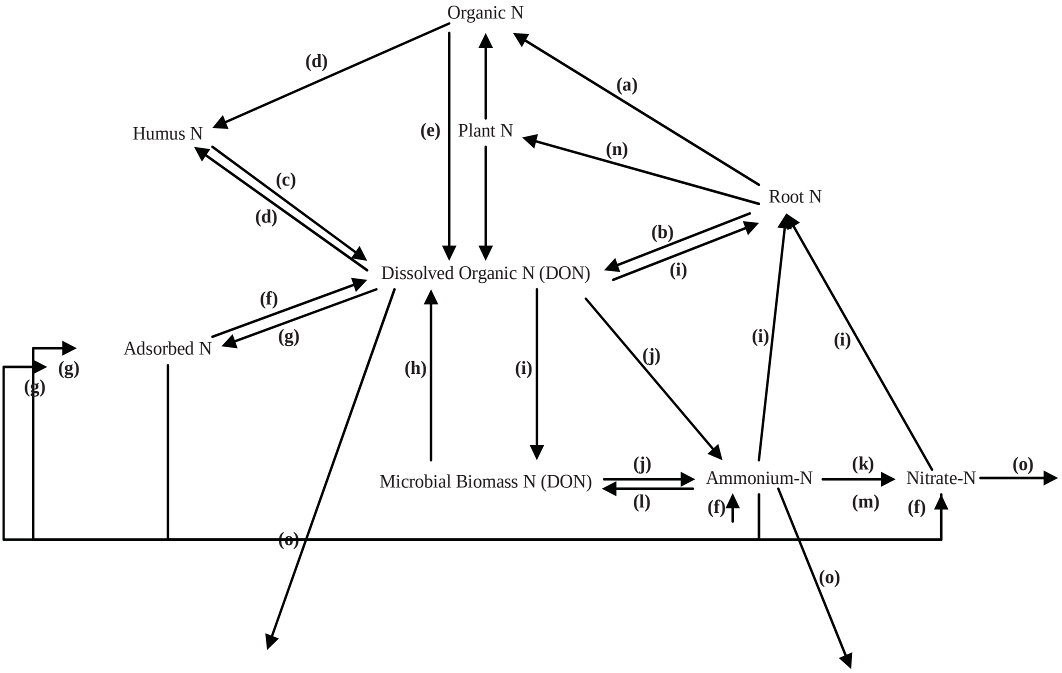

Figure 2. The internal N cycle in a forest ecosystem: a) litterfall and plant debris, b) root exudation, c) decomposition, d) humification, e) solubilization and decomposition, f) desorption, g) adsorption, h) microbial debris, i) assimilation, j) ammonification, k) nitrificatrion, l) ammonium immobilization, m) nitrate immobilization, n) translocation, and o) N export through processes such as leaching, denitrification and volatilization (source: Ketilson, 2004).

The main processes in this internal cycle include mineralization, biotic or abiotic immobilization, nitrification, plant uptake, and return of N through litterfall (Figure 2).

3.1.1. Mineralization/Immobilization of N

Forest soils contain N in both organic and inorganic forms. The organic N is dominant but it is mostly unavailable to tree species (Näsholm et al., 1998). Organic matter is colonized by various heterotrophic soil organisms that derive the energy needed for their growth through the decomposition of organic matter. During this process, N is converted from organic to inorganic form (a process called mineralization); this involves the degradation of protein, amino acids, nucleic acids and other nitrogenous compounds to NH_4^+. In the presence of H_2O, ammonia exists in equilibrium with NH_4^+ as shown in equation (3).

$$\text{R-NH}_2 \xrightleftharpoons{\text{hydrolysis}} \text{NH}_3 + \text{R-OH} \xrightleftharpoons{\text{HOH}} \text{NH}_4^+ + \text{OH}^- \qquad (3)$$

Nitrogen mineralization is carried out by chemoheterotrophic organisms that acquire the required energy for their growth from organic matter, and NH_4^+ is formed as a by-product. Once it is formed, NH_4^+ enters the mineral N pool, along with NH_4^+ derived from atmospheric deposition, and is subject to undergo a number of potential fates, including immobilization, nitrification or adsorption/fixation, as well as being lost from the soil through plant uptake or volatilization. Thus, mineralization is a key process controlling soil N availability for plants, leaching losses, and denitrification (Goulding et al., 1998; Merrington et al., 2002). Conversely, N immobilization is the transformation of N from the inorganic (NH_4^+, NO_3^-) to organic forms in microbial or plant tissues as shown in Figure 2. The balance of mineralization and immobilization determines whether there is a net mineralization or net immobilization in the soil, influencing the supply of NH_4^+ for other N cycle processes (Merrington et al., 2002).

3.1.2. Nitrification

Nitrification describes the biological oxidation of NH_4^+ to NO_3^- or NO_2^-. As the oxidation of NO_2^- is more rapid than that of NH_4^+, there are generally only trace amounts of NO_2^-, which is toxic to plants, in the soil. Nitrate can also be produced directly from organic N through the heterotrophic nitrification process (De Boer and Kowalchuk, 2001). Nitrification can be inhibited mostly by low pH (i.e., < 4.5), low or high temperature (i.e., < 5 °C or > 40 °C), anaerobic conditions, low C and NH_4^+ availabilities, low nitrifier populations, poor competitive ability of nitrifying organisms for NH_4^+, or the presence of allelopathic phenolic compounds (Müller, 2000). The ratio of NH_4^+ to NO_3^- in the soil, therefore, is regulated by the nitrification process. Nitrate also can be lost from forest ecosystems by leaching and denitrification, unless it is taken up by roots or soil microbes (Figure 2).

3.1.3. Denitrification

Denitrification is the reduction of nitrogen oxides (usually nitrate and nitrite) to molecular N or N oxides with a lower oxidation state, induced by bacterial activity or chemical reactions involving nitrite. The latter is specifically defined as chemodenitrification.

Nitrogen oxides are used by bacteria as terminal electron acceptors in place of oxygen in anaerobic or microaerophilic respiratory metabolism (Gunderson, 1991). Conditions with pH 6 ~ 8, and temperature around 20 °C are known to be optimum for denitrification (Paul and Clark, 1996). Conditions favoring denitrification also include the presence of adequate nitrate levels, denitrifying organisms, high soil water contents, low soil oxygen, and poor soil structure, which result in low air filled porosity and anaerobic conditions. The main rate determining factors are known as soil temperature and the amount of readily available C substrate present (Merrington et al., 2002). The diverse pattern of the relative emission rates of $NO:N_2O:N_2$ observed is affected by environmental conditions such as temperature. The $N_2O:N_2$ emission ratio, for instance, increases with decreasing soil temperatures and pH. The high affinity of NO to microbial organisms might even lead to microbial NO consumption, and various enzymes catalyze such transformations (Müller, 2000).

3.1.4. Ammonia Volatilization

Ammonia volatilization occurs as diffusion of NH_3 from soil, plant or liquid systems to the atmosphere. Gaseous losses of ammonia occur in a forest ecosystem through processes such as biomass burning (refer to Table 1). Ammonia losses, resulting from surface volatilization, are aggravated by high NH_3 concentrations in the soil, high soil temperatures, high soil pH and dry conditions. For example, losses of N through ammonia volatilization were between 5 and 40% following application of urea-based fertilizer to a Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) dominated forest in coasted British Columbia (Nason et al., 1988).

Losses of NH_4^+ have been observed in soils with pH 6 to 7 (Stevenson, 1982). Low rates of volatilization are expected from acidic forest soils. However, Craig and Wollum II (1982) reported that despite the high acidity of the forest floor and the mineral soil of a loblolly pine stand, approximately 3.9 to 13.1% of the N added as urea was lost to the atmosphere through ammonia volatilization. They suggested that precipitation trends and seasonal temperature changes might be responsible for ammonia volatilization. Forest burning increases soil pH and may significantly increase NH_3 volatilization loss (Offord, 1999).

3.1.5. Plant Uptake of N

Most plants take up inorganic N forms as ammonium and nitrate, although recent studies have shown that some plants can use simple amino acids and proteins, thereby by-passing the common mineralization pathway (Näsholm et al., 1998). This demonstrates that the ability to take up organic N is a mechanism for boreal plants to adapt to the low N supply. Näsholm et al. (1998) suggested that ectomycorrhizal and ericoid-mycorrhizal plants that can excrete proteases might play a key role in the uptake of organic forms of N.

Plant species also play an important role in N cycling after disturbances such as clear cutting or wildfires. Soil pH increases after the disturbances, and a new microbial community appears, which oxidizes NH_4^+ to NO_3^-. Kronzucker et al. (1997) reported that white spruce (*Picea glauca* (Moench) Voss) seedlings absorbed 20 times more NH_4^+ than NO_3^- from an equimolar solution. Consequently, some major plant species may be at a disadvantage in the presence of abundant NO_3^- in the soil. For example, conifer reforestation projects may be unsuccessful, leading to the domination of disturbed sites by ‘nitrophilous’ species such as aspen (Offord, 1999).

3.2. The Mass Balance of N

Nitrogen enters a forest ecosystem through atmospheric N deposition ($N_{deposition}$) and N fixation ($N_{fixation}$), and exits through harvests, fires, denitrification ($N_{denitrification}$) and leaching ($N_{leaching}$). The sum of N input should be equal to that of N output and accumulation of N by plants (ΔN_{biomas}) in a simple N mass balance equation that can be expressed as follows (Callesen and Gundersen, 2005):

$$N_{fixation} + N_{deposition} = N_{leaching} + N_{denitrification} + \Delta N_{humus} + \Delta N_{biomas} \tag{4}$$

Where ΔN_{humus} means changes in N storage in the forest floor and the mineral soil. Development of a forest floor is the most characteristic feature of forest soils in comparison with agricultural soils. The build-up of semi-decomposed or more humified organic matter is a balance between inputs and mineralization of organic matter. Increased N concentration in litter and in forest floor, and accumulation of soil organic matter may act as a sink for N. Late stage decomposition of organic matter may be slowed down by excessive N inputs and thus allowing soil organic matter to play a greater role as a N sink in areas with high N deposition rates. Disturbances such as fire and harvest may also have an impact on the soil sink for N (Berg and Matzner, 1997; Callesen and Gundersen, 2005). Recently, the N mass balance approach was further ‘improved’ by incorporating terms for the losses through fire, erosion, and ammonia volatilization. This conceptually readily understandable approach has been attractive to both policy makers and scientists. The difficulty when trying to apply it is the lack of adequate data for assigning flux values to each N transport process (Cresser, 2000).

4. EFFECTS OF ATMOSPHERIC N DEPOSITION ON FOREST ECOSYSTEMS

In northern and western Europe, Erisman and de Vries (2000) reported that approximately 50% of the intensive monitoring plots received N inputs above 15 kg ha^{-1} yr^{-1}, a deposition level above which species diversity of the ground vegetation might be negatively affected. Above a deposition threshold of approximately 10 ~ 15 kg N ha^{-1} $year^{-1}$, increased N leaching was also observed in various sites, but the rate of N leaching varied strongly across sites. Nitrate leaching was observed particularly in soils with C/N ratios less than 25 in the humus layer.

Generally, many natural systems are N-limited, particularly those with high carbon accumulation, such as forested peatlands, and therefore may accumulate N. When the plants, animals and microbial biota are unable to utilize all available N, such a system may be considered N-saturated, although there are several different definitions for N saturation (Agren and Bosatta, 1988; Aber et al., 1989; Adams, 2003). Possible symptoms of N saturation include elevated concentrations of soil NO_3^-, soluble Al species and H^+ in surface water, increased incidence of frost damage or other disrupted physiological functions of plants, increased emissions of trace gases, and increased leaching of base cations from forest soils (Aber et al., 1989; Adams, 2003). As the degree of N saturation increases, tree growth may decline and mortality may increase (Adams, 2003).

4.1. Loss of Ca and Other Base Cations

Calcium depletion in forest ecosystems due to acid leaching is a major concern for forest decline, particularly in eastern North America (Likens et al., 1996; Watmough and Dillon, 2003). Low Ca levels have often been associated with reduced tree growth and increased susceptibility to biotic and abiotic stresses including insect defoliation, drought, and extreme cold events. Furthermore, Ca loss in forest soils will lead to declining concentrations of Ca in surface water, a feature that has been reported throughout North America. Recently, Watmougth et al. (2005) reported that despite of reductions in SO_4^{2-} and H^+ deposition, atmospheric deposition continued to acidify soils in many regions of Canada, the United States and Europe, with losses of Ca and Mg being of primary concern. In eastern North America, the estimated losses of Ca caused by acidic deposition over recent decades are believed to pose a major risk to forest health and potential productivity (Lawrence et al., 1995; Likens et al., 1996; Watmough and Dillon, 2003).

Johnson et al. (1994) studied the effects of acid rain on changes in pH and available Ca in soils of the Adirondacks in the USA, and found that moderately acidic organic horizons (pH > 4) showed substantial decrease in pH and available Ca. In addition, Ca concentrations in the strongly acidic organic (pH < 4) and the A horizons significantly decreased, but the pH remained unchanged. Increased leaching of Ca in the later part of the last century mainly resulted from the atmospheric N deposition onto soils of the Adirondacks. In addition, Shortie and Bondietti (1992), in evaluating the trends of exchangeable cations in the acid-sensitive forest sites receiving acidic deposition, and found that measured exchangeable Ca^{2+} and Mg^{2+} prior to 1950 were consistently 150 to 300 $mmol_c\ kg^{-1}$ for organic soil, but consistently below 100 $mmol_c\ kg^{-1}$ after 1970. They concluded that the decrease in exchangeable cations resulted mainly from the increased atmospheric loading of strong acids, as air pollution started to be a concern around 1950 (Bélanger, 2000). Furthermore, Graveland et al. (1994) showed that the accelerated leaching of Ca from the soil decreased Ca availability to snails (as Ca is used to build shells). Then, the decreased Ca availability to the snails led to low Ca levels in the predator (the great tit), resulting in thinner and more porous egg shells. The authors concluded that a poor reproduction in forest passerines resulted from the decline of snail abundance on the acidified soils.

Elevated levels of acidic deposition and subsequent acid leaching can increase base cation losses from forest ecosystems. If such losses of base cations are not replaced through mineral weathering or cation deposition, the soil will become more acidified as the exchangeable base cation pool in the soil diminishes (Levine et al., 1988; van Egmond et al., 2002; Watmough et al., 2005). For example, Bondietti et al. (1989, 1990) observed anomalies in the radial concentration of base cations in stemwood of red spruce (*Picea rubens* Sarg.) stands in New England, Tennessee and North Carolina. Tree rings formed in the mid 1900's showed high levels of base cations, but tree rings formed in the latter part of the century showed significantly lower base cation concentrations. They concluded that the increased levels of base cations were attributed to an increase of base cations in sapwood. The changes in sap chemistry came from an accelerated release of base cations in soil minerals caused by increased atmospheric loading of strong acids around 1950. The decrease in divalent base cations in more recent annual rings can be explained by reduced availability of base cations following the acceleration of leaching losses, and perhaps, by antagonistic effects of Al^{3+} on uptake of base cations (Bélanger, 2000).

The small watershed approach is often useful for the quantitative study of element fluxes, because with appropriate hydrological measurements, relatively precise estimates of chemical inputs and outputs can be obtained. Several calibrated watersheds are currently being monitored throughout eastern North America and Europe, and many reported net losses of base cations in recent decades from forested watersheds (Watmough et al., 2005).

4.2. Acidification

Elevated inputs of N through atmospheric acidic deposition may lead to acidification of soils in forest ecosystems via several pathways depending on the properties of the ecosystems, the form in which N is added, and the anion or cation associated with the added N. Added N can cause soil acidification regardless of the form by which it is added, but the net change in soil acidity due to N inputs depends on plant uptake of N (Matson et al., 1999).

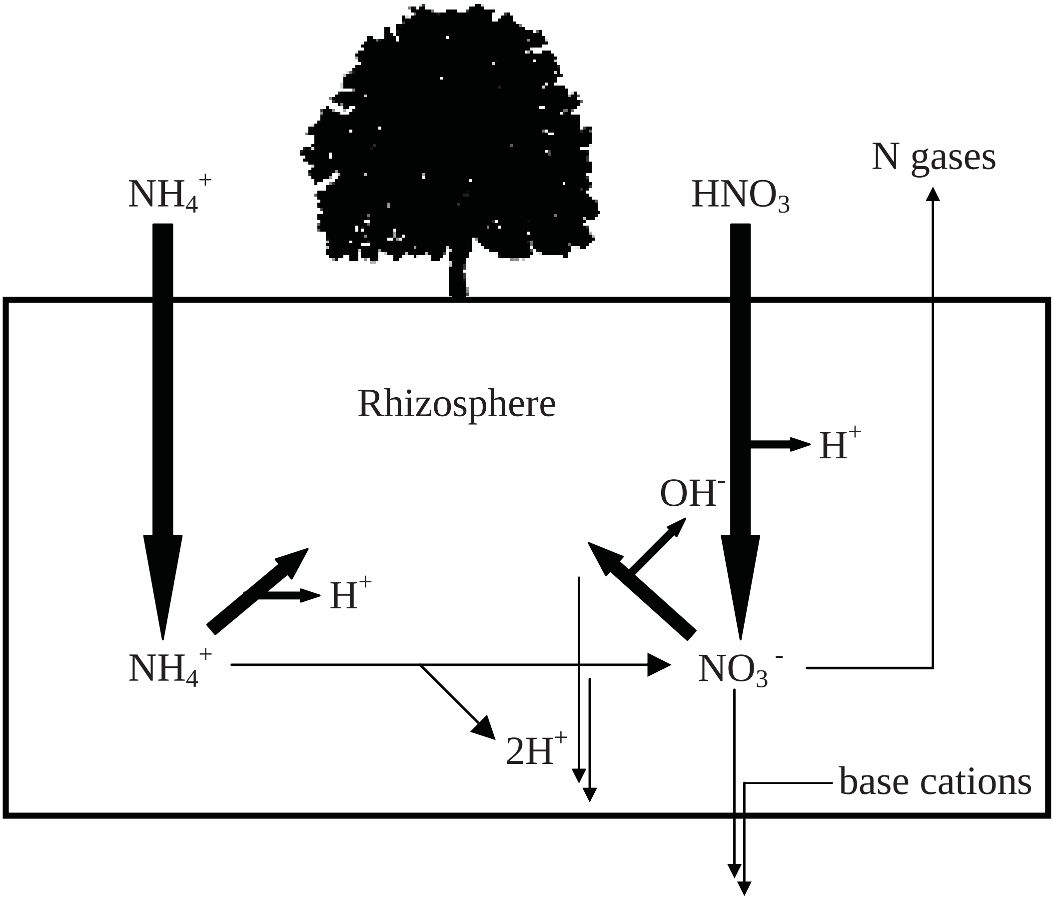

Figure 3. Effects of atmospheric N deposition on N cycling in non-N-saturated forest ecosystems. The thickness of the arrows represents the relative magnitude of fluxes of N in the diagram (source: Matson et al., 1999).

As shown in Figure 3, nitric acid inputs do not necessarily lead to soil acidification, because if the NO_3^- is taken up by plants, the H^+ is neutralized by the OH^- released by plants. However, if NO_3^- remains mobile in the soil, and leaches out of the system, the greater affinity of H^+ for soil exchange sites will displace base cations such as Ca and Mg which will then accompany NO_3^- in the leaching process. In temperate ecosystems, addition of excess N from the atmosphere has led to soil acidification and base cation depletion, although strong plant demand for N slows the rate of change. Moist tropical forest systems, however, are frequently rich in N relative to other essential elements, and leaching of NO_3^- from surface soil mobilizes cations, H^+ and Al species, causing potentially serious consequences (Matson et al., 1999).

Soil acidification influences nutrient availability in the soil through processes such as loss of base cations and increase of Al and Mn concentrations in soil solution, in addition to the direct effect of soil pH on nutrient form and availability. Johnson and Siccama (1983) also reported that nutrient availability could increase in the earlier stages of soil acidification due to the release of cations into the soil solution by increased metal solubility, but this short-term effect can rapidly disappear with the leaching of cations and subsequent release of metals such as Al^{3+} into the soil solution.

4.3. N Saturation

Forest soils receiving low to moderate levels of N deposition retain most of the deposited N, although several people expressed concerns that gradual accumulation of N in forest soils may lead to N-saturation (N input exceeds the biotic demand), causing an increase in NO_3^- leaching, and undermining the benefits resulting from decreased S emissions (Aber et al., 1989; Bringmark and Kvarnas, 1995). The concept of N saturation was established in 1981, when Ingestad et al. (1981) presented a simple model of N nutrition, based on the nutrient flux density and N productivity concepts. The model was used to predict N nutrition, when N additions would be sufficient to remove all N limitations on forest growth under typical conditions in Sweden. Nihlgard (1985) suggested that excess N availability might be a serious concern for both forest health, and acidification of soil and stream water.

The ammonium hypothesis suggested by Nihlgard (1985) marked the beginning of the focused discussion of the potential environmental impacts of excessive N deposition. Nitrogen saturation can be defined as the availability of NH_4^+ and NO_3^- in excess of total combined plant and microbial nutritional demand (this definition excludes the use of NO_3^- as a substrate for denitrification). By this definition, N saturation can be determined simply by the accumulation of mineral N in the soil (generally as NH_4^+ in humid areas) or by increased leaching of NO_3^- or NH_4^+ below the rooting zone. Saturation implies limitations on biotic function by the availability of other resources such as P or water for plants, and C for microbes (Aber et al., 1989).

Aber et al. (1989) suggested four stages in the development of N saturation: (1) characteristic N cycling under N-limiting conditions, (2) initial effects of chronic N deposition, (3) N saturation, and (4) forest decline. Aber (1992) identified that N saturation could cause serious impacts on: (1) soil chemical properties and water quality, (2) forest composition and productivity, and (3) greenhouse gas fluxes. Aber (1992) proposed general properties of N-limited and N-saturated forest ecosystems as two end-points with the understanding that movement from one end-point to the other would be continuous (refer to Table 2). Predicting the timing of N saturation in relation to rates of N deposition is crucial for the establishment of critical loads of N for acid-sensitive systems (Aber, 1992).

4.4. Leaching Losses of Ammonium and Nitrate

Concerns were raised in the late 1980s that high N deposition and the resulting N-saturation might increase nitrate leaching, generally above a critical deposition threshold of around 10 kg N ha^{-1} yr^{-1} (Erisman and de Vries, 2000; Watmough et al., 2005). Reduced C:N ratios and subsequently increased nitrate leaching following N deposition has been proposed as a mechanism for forest decline. There is considerable variation in N leaching losses among locations receiving similar levels of N deposition, depending on forest species composition and site characteristics. Nevertheless, concerns still remain that chronic accumulation of N in forest soils may ultimately lead to N-saturation and increased nitrate leaching (Aber et al., 1989; Watmough et al., 2005).

In recent years, forest floor C:N ratios have been proposed as an indicator of nitrate leaching in forest ecosystems as a result of chronic N deposition (Dise et al., 1998). While NH_4^+ availability is generally low in N-poor systems, it is increased by N deposition. Increased NH_4^+ availability has the dual effect of promoting nitrification and inhibiting NO_3^- immobilization, because NH_4^+ is preferentially immobilized by microbes (Müller, 2000). Therefore, NO_3^- immobilization is reduced despite of increased NO_3^- availability from the deposition. With sufficiently high inputs of inorganic N, NO_3^- will accumulate in forest soils, and the potential for leaching will increase (Curtis et al., 2004). For example, Curtis et al. (2004) reported that C:N ratio was inversely related to modeled inorganic N deposition and measured nitrate leaching for three of the four catchments they studied. They concluded that the C:N ratio of surface organic matter is a potential indicator of N saturation and leaching in some systems. Nitrate leaching is also an environmental concern because of potential adverse effects on soil chemical processes and surface water quality in old-growth forest ecosystems (Garten Jr., 2000).

Forest ecosystems receiving intermediate levels of N deposition may not show obvious symptoms of forest decline, but nitrification may begin to increase nitrate levels in the soil and water. Because leaching of significant levels of nitrate is associated with symptoms of forest decline, annual export flux of nitrate in runoff also can be used as an indicator of forest ecosystem health (Dise et al., 1998; Aber et al., 1989). For example, Matzner and Grosholdz (1997) found a good relationship between the organic horizon C:N ratio and output flux of nitrate in 16 spruce forest sites, mostly in Germany. Dise et al. (1998) evaluated a hypothesis that C:N ratio of organic horizon could be used to estimate the level of nitrate leaching in 33 conifer forests across Europe. The authors showed that at intermediate (10 ~ 20 kg N ha^{-1} $year^{-1}$) and high (> 20 kg N ha^{-1} $year^{-1}$) N deposition rates, nitrate leaching increased with decreasing soil C:N ratio. In addition, for any given value of C:N ratio, the level of nitrate leaching was greater at high than at intermediate N-deposition sites. However, at even higher N-deposition sites (> 30 kg N ha^{-1} $year^{-1}$), the data were highly variable suggesting that other factors may affect nitrate leaching. Gunderson et al. (1998) reported that the risk of nitrate leaching is low for sites with organic horizon C:N ratio above 30, moderate if between 25 and 30, and high for those less than 25, based on data from Denmark, the Netherlands, and northern and central Europe.

Table 2. Characteristics of N-limited and N-saturated forest ecosystems

Characteristic	N-limited	N-saturated
Form of N cycled (net, as plant uptake)	100% NH_4^+	25-50% NO_3^- 50-75% NH_4^+
Soil DOC concentration	High	Low
Ratio of gross NO_3^- immobilization to gross nitrification	Near 100%	Near 0%
Ratio of gross NH_4^+ immobilization to gross mineralization	High (90-95%)	Low (50%)
Fraction of soil fungi that are mycorrhizal	High	Low
Nitrate loss during snow melt	Low	High
Nitrate loss at base flow	Zero	High
Foliar lignin concentration	High	Low
Foliar N concentration	Low	High
Foliar free amino acid (e.g. arginine) concentration	Zero	High
Soil C:N ratio	High	Low
N_2O production	Zero	High
CH_4 production	High	Low (zero)

Source: Aber, 1992.

4.5. Aluminum Toxicity

Atmospheric N deposition and the resultant soil acidification can increase the concentration of soluble Al in soil solution. Aluminum ions released during the soil acidification process will further lower forest soil pH and cause leaching of essential plant nutrients such as Ca, Mg and K. The major species of Al is the Al^{3+} ion when pH is less than 4, which can cause toxic effects to woody plants, through exerting an antagonistic effect on tree growth by inhibiting the uptake of mineral nutrients such as Ca and Mg (Figure 4).

Toxicity to trees in forest ecosystems is also frequently associated with increased levels of Al, Fe, Mn, and possibly other heavy metals, which may exert an adverse effect on trees in acid forest soils. Additions of Ca- and Mg-containing fertilizers to acidic forest soils can greatly alleviate Al toxicity to trees (Kabata-Pendias and Pendias, 2001).

The molar ratio of Ca to Al in forest soil solution is often used to monitor soil acidification and Al toxicity to trees, of which both can be causes for forest decline. For example, soil solution Ca/Al molar ratios below 1 were shown to reduce tree growth by 50% or to cause imbalance of the nutritional status of trees (Cronan and Grigal, 1995; van Schöll et al., 2004). The ratio also can be used as an index for determining an acceptable load of long-term atmospheric N deposition in forest ecosystems.

Plants are adversely affected by exposure to ionic Al species either through antagonistic interference with cation uptake or through irreversible damage to plant cells, especially roots, from Al interactions with sensitive biomolecules. Most scientists agree that roots strongly adsorb Al by an exchange phenomenon or by formation of relatively insoluble organo-Al complexes involving mucilage produced at root tips (Cronan and Grigal, 1995). Another point of agreement is that cations compete for root adsorption sites, with Ca and Al regarded as the two most prominent competitors. The presence of Al in solution, or more specifically Al adsorbed on cell walls or membranes, markedly interferes with the uptake of other cations. Aluminum rich solutions can reduce Ca and Mg concentrations in the apoplast and interfere with their uptake.

As a result, many of the symptoms of Al toxicity are those associated with Ca or Mg deficiencies (Edwards et al., 1976; Cronan and Grigal, 1995).

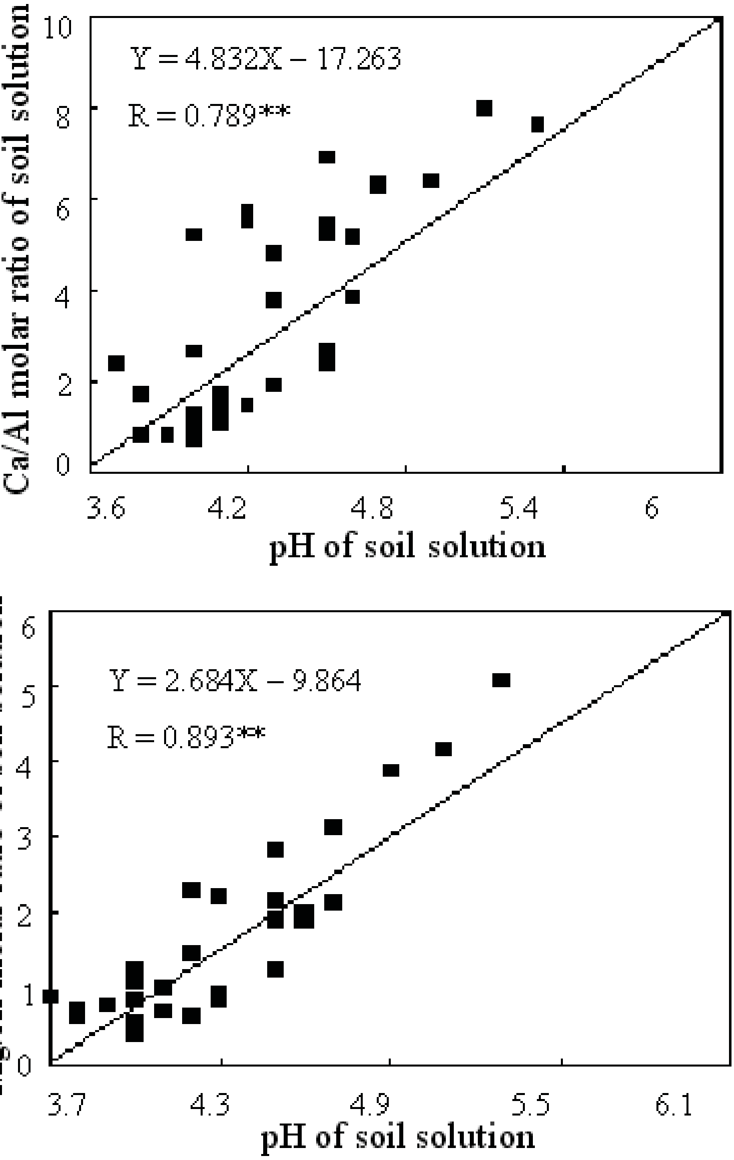

Figure 4. Relationships between pH and Mg (or Ca)/Al of forest soil solutions receiving continuous inputs of atmospheric acidic deposition (source: Lee et al., 2004a).

4.6. The Health of Forests and Trees

Increased N deposition to N-limited forests may initially increase forest growth. However, excessive N inputs might result in severe imbalances in element concentrations causing foliar chlorosis, premature needle drop, and decline of tree vigor, and even mortality (Aber, 1992). The imbalances can be aggravated by soil leaching, which reduces Mg, but increases Al concentrations in forest soils, which in turn can reduce plant uptake of Mg^{2+} and other cations. High foliar N concentrations have also been implicated in forest decline under N saturation conditions through the loss of frost-hardiness and increased winter desiccation (Aber, 1992). Aluminum toxicity may reduce fine root growth, and the reduced fine-root biomass could have important implications for plant uptake of other resources, particularly water and P. Both reduced root mass and mycorrhizal infection are common characteristics of declining vigor of conifer forests in both Europe and the United States (Kraske and Fernandez, 1990). Low foliar P content has been noted of conifers in high deposition areas in the United States (Bytnerowicz and Fennn, 1996). Drought has been implicated in either triggering or exacerbating forest decline (Aber et al., 1989). Annual assessment of the crown condition of forest trees in Europe revealed a general increase in defoliation and discoloration of foliage (Erisman and de Vries, 2000). The adverse effects of air pollution may appear after a considerable time, especially when concentrations of pollutants are low. At present, most scientists agree that the state of forests is influenced by a multitude of different stress factors that include air pollution. The dynamics of the impact of stresses on forests are, however, only partially understood, because of the non-linear characteristics of the response of vegetation (Erisman and de Vries, 2000).

5. CRITICAL LOADS OF ATMOSPHERIC N DEPOSITION

5.1. The Critical Load Concept

Critical load is a quantitative estimate of an exposure to one or more pollutants, below which significant harmful effects on specified elements of the environment do not occur according to present knowledge (Bull, 1993), or it can be defined more simply as the maximum load of atmospheric pollutant that sensitive ecological systems can tolerate without occurring long-term harmful effects. This concept has been applied mainly to NO_x and SO_2 depositions, to indicate the capacity of soils in sensitive environmental region to buffer atmospheric acidic inputs (Merrington et al., 2002). The critical load for soils in specific areas depends on a number of factors such as soil parent material, soil texture, soil depth, drainage, slope, base cation deposition from the atmosphere, annual precipitation, and tree species or vegetation type. If all other factors are equal, a shallow and freely draining soil on a steeper slope in a high rainfall area with low atmosphere non-marine base cation deposition will be more sensitive to acidification (Nilsson and Grennfelt, 1988; Cresser, 2000).

Attempts have subsequently been made to relate harmful chemical effects to biological responses, for example, by setting a critical load to ensure that the base cation to aluminum ratio in soil solutions do not fall into a range low enough to cause damage to fine roots of plants (Cresser, 2000). The mass balance of base cations has been used to calculate a critical load for soil acidity. However, critical loads for N inputs are difficult to determine (N compounds, such as NH_3, can both acidify the soil and act as a plant nutrient), but have been estimated at 5 ~ 45 kg ha^{-1} $year^{-1}$ for a range of ecosystems from heathland to forests. In general, the lower the soil buffering capacity and the sparser the vegetation, the lower the critical load. Some natural and semi-natural ecosystems are likely receiving much more N than their critical loads for N and this likely causes changes in the flora and fauna of the ecosystems due to the increased N supply, and increased soil acidification as the deposited NH_3 is nitrified and releases H^+ ions into the soil solution (Merrington et al., 2002). Therefore, there is an urgent need for long-term research and monitoring on N deposition and the determination of critical loads of N in different ecosystems. Such research programs exist including the Long-Term Ecological Research Program (LTER) and Intensive Site Ecosystem Monitoring Program (ISEM) by the US Forest Service (Adams, 2003). Continued support for such research programs is essential for improving our understanding of the impact of N deposition on forest ecosystem health and to better manage N emissions.

Steady-state critical load models for acidic deposition have been developed to evaluate the potential threat of acidic deposition to forest ecosystems. These models allow soils to acidify, but only to a limit determined by a critical chemical criterion, usually a specified base cation-to-aluminum ratio in soil solution (Watmough et al., 2005). In reality, the spatial distribution of weathering inputs of base cations throughout soil profiles needs to be considered in the context of root distributions, since much weathering may occur below the main rooting zone. Other complicating factors in the calculation of critical load are uncertainties about the medium- to long-term changes in soil organic horizons, and the lack of definitive statements about the time scale being considered.

When a forest ecosystem has reached N saturation, N deposition ($N_{deposition}$, a critical deposition level) and N input through N fixation ($N_{fixation}$) have to be equal to or less than the annual uptake capacity in biomass (ΔN_{biomas}), the increase in soil organic N (ΔN_{humus}), plus the N lost in denitrification ($N_{denitrification}$) and leaching ($N_{leaching}$). Thus, the critical deposition ($N_{crit\ depos}$) can be expressed as follows (Callesen and Gundersen, 2005):

$$N_{crit\ depos} = N_{leaching} + N_{denitrification} + \Delta N_{humus} + \Delta N_{biomas} - N_{fixation} \tag{5}$$

In assessing the critical loads of N for terrestrial ecosystems, scientists initially opted to base their assessment on protection from long-term chemical changes with respect to base saturation (Hodson et al., 1997). Thus, the amount of base cations leached or taken up by growing forest trees had to be equal to, or less than, the sum of weathering-derived and deposited base cations. They then assumed that only sulfate or nitrate accompanies base cations that are leached. This ignores the role played by HCO_3, and organic complexation of Ca^{2+} and Mg^{2+}, which when considered together, clearly could result in a serious error. They also ignore the fact that ammonium deposition may directly displace base cations from cation exchange sites in acid-sensitive soils, resulting in their increased movement down the soil profile, and possibly out of the rooting zone, although the associated risk of NH_4-K or NH_4-Mg imbalances was discussed in a later report by the Nordic Council of Ministers (Cresser, 2000).

Table 3. An example classification of soil acidity using pH, % base saturation and soluble Al concentration

Class	Acidity	pH_{H2O}	Base saturation %	Soluble Al cmol kg^{-1}
1	Low	> 5.5	> 50	< 0.3
2	Moderate	4.4 ~ 5.5	10 ~ 50	0.3 ~ 1.0
3	High	4.0 ~ 4.4	6 ~ 10	1.0 ~ 1.2
4	Very high	< 4.0	< 6	> 1.2

Source: SwEPA, 2000.

5.2. Indicators and their Thresholds of Acidification for Forest Ecosystems

Processes to establish critical loads depend on the selection of chemical criteria. For forest soils, these criteria can be parameters such as soil pH, base saturation, Al or base cation concentrations in soil solution, and the ratios of base cation to Al concentrations. For each chemical criterion, critical values (or thresholds) need to be determined. Table 3 shows one example of criteria used to assess soil acidity in Sweden (SwEPA, 2000). The soil is assigned the acidity classification from low to very high based on pH measured in water, % base saturation, and soluble Al concentration.

5.2.1. Soil pH

Measuring soil pH in $CaCl_2$ solution is probably one of the most commonly used method to characterize soil acidity. The use of $CaCl_2$ has advantages over water for pH measurement (Hendershot et al., 1993; Thomas, 1996): (1) the pH is not affected within a range of soil-to-solution ratios, (2) the pH is almost independent of soluble salt concentrations for non-saline soils, and (3) soil pH is not affected whether moist or air-dried soils are used. Ok et al. (2006) evaluated relationships among pH, % base cation saturation and soluble Al concentration in forest soils. They reported that chemical properties related to base cations such as base saturation (%) and Ca or Mg saturation (%) showed positive relationships with pH, and Al saturation showed a negative relationship with pH in water or 0.01M $CaCl_2$. Ulrich et al. (1984) suggested that soil pH_{H2O} between 4.0 and 4.2 poses a high risk of damage to forest ecosystems. Recently, Turchenek and Abboud (2001) suggested that the critical pH_{H2O} is 5.6, which is equivalent to a pH_{CaCl2} of about 5.0 for soils in the oil sands region in Alberta.

5.2.2. Base Saturation (%)

Base saturation is the ratio (expressed as a percent) of the quantity of exchangeable bases to the cation exchange capacity (CEC) of the soil. The base saturation of a forest soil has ecological significance, because the ratio of base cations to total cations on the exchange sites determines their ratio in the soil solution and thus their availability for plant uptake. The toxic levels of metal cations in the soil solution depend primarily on their ratio to base cations, especially Ca. The ratio of Ca/Al, for example, is related to tree growth and root activity, so that the assessment of this molar ratio in the soil solution may provide a useful measure of Al toxicity (Meiwes et al., 1986). For forest ecosystems, base saturations of 5 and 15% were recommended by Ulrich et al. (1984) and Cronan and Grigal (1995), respectively, as thresholds for causing negative effects due to soil acidification.

5.2.3. Aluminum Concentration and Base Cation to Al Ratio

Most of the exchangeable acidity in the soil, particularly in the mineral soil, is considered to exist as exchangeable Al species, especially as Al^{3+}. Reuss and Johnson (1986) reported that 1) as exchangeable base cations are depleted in the soil by leaching or soil acidification processes, Al rather abruptly becomes dominant in the soil solution, 2) as the fraction of cation-exchange sites that are occupied by (Ca + Mg) decreases, the Ca/Al and Mg/Al ratios in soil solution decline, and 3) as total solution ionic strength increases, Al^{3+} concentration in solution also increases. Such changes in the soil might result from atmospheric acidic deposition or long-term soil acidification, producing a gradually decreasing pattern for Ca/Al ratio in the soil solution (Cronan and Grigal, 1995).

Table 4. Correlation coefficients for chemical parameters and nutrient concentrations between soil solution and two-year-old needles of *Pinus thunbergii*

Soil solution	Two-year-old needles					
(A Horizon)	Ca	Mg	Al	Mn	Ca/Al	Mg/Al
Ca	ns	ns	ns	-0.40**	ns	ns
Mg	ns	0.43**	-0.40**	-0.42**	0.45**	0.55**
Al	-0.42**	-0.42**	ns	Ns	-0.41**	-0.37*
Mn	-0.38*	-0.33*	ns	0.40**	ns	ns
pH	0.39*	0.56**	-0.47**	-0.47**	0.62**	0.63**
Ca/Al	ns	0.54**	-0.52**	-0.52**	0.73**	0.75**
Mg/Al	ns	0.60**	-0.48**	-0.48**	0.74**	0.82**
Mg/Mn	ns	0.39*	-0.47**	-0.47**	ns	ns

ns: not significant.

*, ** refer to significance at $\alpha = 0.05$ and 0.01, respectively.

Source: Lee et al., 2004b.

Table 5. Indicators for assessing whether an ecosystem has a high probability of suffering from Al stress

Indicator	Threshold
Soil base saturation	< 15% of effective CEC
Soil solution Ca^{2+}/Al_i molar ratio	1.0 (50% risk)
	0.5 (75% risk)
	0.2 (95-100% risk)
Fine root Ca/Al molar ratio	0.2 (50% risk)
	0.1 (80% risk)
Current foliar Ca/Al molar ratio	12.5 (50% risk)
	6.2 (75% risk)

Source: Cronan and Grigal, 1995.

Nutrient concentrations in soil solution are often related to nutrient concentrations in the vegetation (Table 4). In this example, Ca concentrations in the soil solution of A horizon from sites near industrial complexes were negatively correlated with Mn concentrations in two-year-old needles of *Pinus thunbergii*. Moreover, Mg concentrations in soil solutions showed negative correlations with Al and Mn concentrations in pine needles. The Mg concentration in needles decreased as soil pH decreased (Table 4).

Different thresholds of base cation to Al ratio have been suggested to assess the impact of soil acidification on tree growth (Ulrich, 1984; Bloom and Grigal, 1985; Levine and Ciolkosz, 1988; Turchenek and Abboud, 2001). For example, Sverdrup and Warfvinge (1993) presented response curves of growth of various trees and ground vegetation species in relation to base cation (BC)/Al ratio, based on a literature review. The critical BC/Al ratios, at which growth of various grasses was negatively affected, ranged widely from 0.3 to 300 with a mean value of 10 depending on the grass species. Considering the fact that the critical value is less than 45 for most species, a value of 45 was selected to evaluate the effect of soil acidification by Turchenek and Abboud (2001).

In their review, Cronan and Grigal (1995) suggested four indicators to set thresholds for assessing potential impact of Al stress on forests (Table 5): 1) soil base saturation less than 15% of effective CEC, 2) soil solution Ca/Al molar ratio ≤ 1.0 (for 50% risk), 3) fine root tissue Ca/Al molar ratio ≤ 0.2 (for 50% risk), or 4) a foliar Ca/Al molar ratio ≤ 12.5 (for 50% risk). This may provide a means of distinguishing site conditions, where Al stress is likely to adversely affect tree growth. Cronan and Grigal (1995) showed that soil solution Ca/Al molar ratio could provide a valuable tool for estimating the approximate threshold, beyond which the risk of forest damage from Al stress and nutrient imbalances will dramatically increase. Moreover, the Ca/Al ratio may be used as an indicator to assess changes of a forest ecosystem over time in response to acidic deposition or other processes contributing to acid soil infertility. It should be noted that the 'Ca/Al model' refers to the soil solution, but the composition of soil solution is generally in equilibrium with exchangeable cations. Trees may be able to extract the nutrients from the mineral soil despite the presence of high levels of Al^{3+} refuting the model prediction that Al^{3+} on exchange sites on and in the plant cell wall would block the uptake of base cations (Högberg et al., 2006). Therefore, further research is needed to validate the use of this indicator for soil acidification study.

5.2.4. Acid-Buffering Capacity

For acidic soils, the acid-buffering capacity provides a measure of the amounts of bases required to neutralize protons present in soils. It is sometimes described as the lime requirement of soils, and depends primarily on the amount of acid cations (mostly as exchangeable cations) present in the soil. Recently, Ok et al. (2006) estimated soil acid-buffering capacity using an acetic acid equilibrium procedure by measuring pH after acetic acid treatment. They found that the pH after acetic acid treatment was highest in the forest floor (pH 2.70 to 3.15) among samples collected from different horizons, mainly due to its high organic matter content. The acetic acid equilibrium procedure was evaluated by Ashworth and Kirk (1999) for monitoring changes in acid-buffering capacity of topsoils in an area exposed to acidic emissions in Alberta. They reported that pH values after acetic acid treatment ranged from 2.65 to 3.39 for topsoils collected in 1997. The acid buffering capacity of soils is also strongly influenced by the type of parent material. Table 6 shows a classification of rock type according to their ability to buffer acidic inputs.

Table 6. The acid neutralizing potential of rock types

Group	Acid neutralizing potential	Rock type
A	None ~ low	Granite, syenite, granite-gneisses, quartz sandstones (and their metamorphic equivalent) and other siliceous (acid) rocks, grits, orthoquartz, decalcified sandstones, some quaternary sands/drifts
B	Low ~ medium	Sandstones, shales, conglomerates, high grade metamorphic felsic to intermediate igneous, calc-silicate gneisses with no free carbonates, metasediments free of carbonates, coal measures
C	Medium ~ high	Slightly calcareous rocks, low-grade intermediate to volcanic ultramafic, glassy volcanic, basic and ultrabasic rocks, calcareous sandstones, most drift and beach deposits, mudstones, marlstones
D	“Infinite”	Highly fossilferous sediment (or metamorphic equivalent), limestones, dolostones

Source: Tao and Feng, 2000.

5.2.5. Acid Neutralizing Capacity (ANC)

Meiwes et al. (1986) classified forest soils into six buffer ranges according to the mechanism of acid-buffering (Table 7). Their classification is based on consideration of the solubility of the buffering compounds, the dominance and ecological importance of certain ions and the corresponding pH-values in the soil solution. Meiwes et al. (1986) also suggested parameters that can be potentially used to assess the sensitivity of forest soils to acidification (Table 9). Soils with equivalent [H + Fe] fractions greater than 0.02 in the mineral and 0.05 in the organic matter rich horizons are considered to have been affected by a recent phase of acidification. Protons are usually buffered at a fast rate so that their presence in significant amounts in the soil indicates either a recent production of proton in forest ecosystems or low capacity of the forest soil to buffer proton. However, the classification in Table 8 was based on data compiled mostly from northwestern German soils, and thus further validation is needed to use the classification for general soil acidification studies.

Mapping of soil sensitivity to atmospheric acidic deposition has become an important task in order to locate areas most susceptible to environmental impact. A number of maps have been generated to identify sensitive soils using different types of criteria and soils information (Tao and Feng, 2000). However, such maps were generated using only static soil parameters at a single point in time to determine soil sensitivity to acidic deposition, and do not account for dynamic, temporal changes that are naturally occurring within a soil profile; such temporal changes interact with acidic deposition (Levine and Ciolkosz, 1988).

Table 7. Grouping of well aerated and drained forest soils into soil buffering ranges, and their possible buffering reactions, buffering capacities and other soil and plant characteristics

Soil buffer range	Possible buffer reactions	Buffering capacity1) (kmol H^+ ha^{-1} of surface 0.1 m)	Soil and plant condition
Calcium carbonate (pH 6.2 ~ 8.0)	$CaCO_3 + H_2O + CO_2 (g) \leftrightarrow Ca^{2+} + 2HCO_3^-$	150-300 per % of $CaCO_3$	Mull-type humus form; high turnover rate of litter; stable, crumb-like structure, leaching of mainly Ca and HCO_3, low solubility of trace metals; possible depressed ion uptake because of unbalanced ratios of Ca/K and cations/anions; absence of toxins like Al or phenols
Silicate buffer (pH 5.0 ~ 6.2)	$CaAl_2Si_2O_5 + 2H_2CO_3 + H_2O \rightarrow Ca^{2+} + 2HCO_3^- + Al_2Si_2O_5(OH)_4$	25-75 per % silicate	Mull-type humus form; high turnover rate of litter; less stable structure (due to migration of clay particles); reduced leaching of nutrients, well-balanced and adequate nutrient supply
Cation exchange buffer (pH 4.2 ~ 5.0)	$[AlOOH]_n$ (clay lattice) + $0.5nH^+ + nH_2O \rightarrow [Al(OH)_{2.50}^{0.5+}]n$ (clay interlayer) + $0.5n\ H_2O$	7 per % clay	Accumulation of a top humus layer of the moder type, reduced biological activity, increased stability of soil structure with increasing equivalent fraction of exchangeable Al; decreased pools of basic cations by cation exchange and leaching; reduced growth and exclusion of calcicolous plants by acid toxicity
Aluminum buffer (pH 3.8 ~ 4.2)	$[Al(OH)_2(H_2O)_4]^+ + H_3O^+ \leftrightarrow [Al(OH)(H_2O)_5]^{2+} + H_2O$	100-150 per % clay	Top humus layer of moder type; low biological activity and low turnover rates of litter, stable soil structure; low storage of basic exchangeable cations; leaching of Al and Mn; probable toxic effects to all plant species by acidity
Aluminum-iron buffer (pH 3.0 ~ 3.8)	See aluminum or iron buffers	-2)	Raw humus type, very low biological activity and very low turnover rates of litter; very low ion availability in the mineral soil; high probability of acid toxicity
Iron buffer (pH 2.4 ~ 3.0)	$[Fe(OH)_2(H_2O)_4]^+ + H_3O^+ \leftrightarrow [Fe(OH)(H_2O)_5]^{2+} + H_2O$	-	Raw humus type; very low ion availability in the mineral soil, fine roots confined only to the organic layer at the soil surface

1) Calculated for the fine soil fraction with a bulk density of 1 g cm^{-3}.

2) Not available.

Source: Meiwes et al., 1986.

Table 8. Classification of pH and the equivalent contribution of cations (X^s, as a ratio) to the exchange capacity (CEC_e) as measures of the elasticity of soils (with $CEC_e > 0.5$ cmol kg^{-1} soil), with respect to acid toxicity and the supply of K and Mg to tree species tolerant to acidity

Toxicity due to acidity	pH_{H2O}	$X^s_{Ca} + X^s_{Mg}$	$X^s_H + X^s_{Fe}$	X^s_{Al}	X^s_K or X^s_{Mg}	Elasticity[1)]
Unlikely	> 5.0	> 0.5	< 0.02	< 0.3	> 0.04	very high
Possible	4.2-5.0	0.15-0.5	< 0.02	0.3-0.6	0.02-0.04	high
Probable	3.8-4.2	0.05-0.15	< 0.02	0.6-0.8	0.01-0.02	low
Highly probable	< 3.8	< 0.05	0.02-0.05	> 0.8	< 0.01	very low

[1)] The elasticity of an ecosystem is defined by parameters which characterize the ability of the system to react to the imposed stress. Even weak stresses may cause significant changes in ecosystems of low elasticity.

Soils with $CEC_e > 0.5$ cmol kg^{-1} soil are considered to have very low elasticity (source: Meiwes et al., 1986)

6. CONCLUSIONS

Atmospheric deposition of N has gained ecological significance especially during the last two decades, partly because of the steady decline of S emissions and partly because of increased NO_x emissions. Nitrogen deposition is regarded as a threat to forest ecosystems particularly in densely populated regions of Europe and North America. In addition, accelerated industrialization now makes atmospheric N deposition more significant in other parts of the world such as Asia and Latin America. Nitrogen deposition affects both tree growth and the environment, as deposited N contributes to gradual acidification of soil and water bodies. Atmospheric N deposition may cause biotic stresses in forest ecosystems by 1) depleting base cations in soils, 2) promoting soil acidification, and 3) increasing concentrations of strongly acidic anions and ionic Al and Mn concentrations in soil solution. These processes can lead to an increase in the incidence and severity of Al toxicity and antagonism, and nutrient imbalances in forest ecosystems. In effect, these processes can promote infertility of acid soils, which is characterized by concurrent H^+ or Al toxicities, and deficiencies of Ca and Mg.

In industrialized regions, atmospheric N deposition has clearly been shown to accelerate soil acidification, and in many cases N saturation. Direct effects of acid deposition on soils include positive effects, such as increased N availability, and negative effects such as leaching of soil nutrients and heavy metal toxicity. Biological processes play an important role in soil acidification, as N compounds from atmospheric deposition all undergo nutrient cycling processes. In many slightly polluted areas, soil acidification has been found to be caused mainly by internal biological processes, i.e., cation uptake and accumulation in biomass was responsible for up to 87% of soil acidification (Marcos and Lancho, 2002). However, the impact of N transformation is often overlooked in soil acidification studies. Better predictions of ecosystem responses to atmospheric N deposition require an improved understanding of biogeochemical processes such as base cation leaching that affect N cycling in ecosystems.

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Chapter 4

USING BUGS (HEMIPTERA) AS ECOLOGICAL AND ENVIRONMENTAL INDICATORS IN FOREST ECOSYSTEMS

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ABSTRACT

Many orders and families of invertebrates have been promoted as ecological and environmental indicators of management practices and natural disturbances in forest ecosystems. To date most research has focused on ants, particularly for gauging the success of efforts to restore lands modified by human disturbance. However, it is now recognised that a range of taxa are potentially required. Here, beetles, butterflies, ants and spiders have received interest as potential candidates for the 'shopping basket'. Less well known, but of great importance, are responses by the hyperdiverse order Hemiptera (true bugs). Recent research along a latitudinal gradient shows Hemiptera to be one of the best orders of invertebrate at discriminating between different forest types. This paper reviews the benefits of incorporating Hemiptera into ecological studies examining forest management practices. We describe the contribution Hemiptera make as the fifth most speciose insect order to forest biodiversity, their functional role in ecosystems, and their role as forest pests. Hemiptera occur in all forest strata (e.g., soil, leaf-litter, understorey, overstorey). As abundant and diverse prey they are likely to contribute to the high diversity of other arthropods plus insectivorous birds, mammals and reptiles. Although most Hemiptera are herbivorous, the group exhibits a wide spectrum of feeding habits, including predators, fungivores, and parasites. Even within the herbivores there is great

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variation owing to different host specificity levels, with some species highly monophagous (feeding only from one species of plant), through to species that are highly polyphagous (feeding from different families of plants). As many polyphagous Hemiptera often target plants with high nutrients, individual plants within a species may also differ in their hemipteran assemblages owing to differences in nutrients. This diversity in trophic requirements means that Hemiptera are sensitive to changes not only in habitat structure, but also floristics and changes in plant chemistry. Similarly, seasonal changes can also influence the structure of hemipteran assemblages at spatial scales ranging from individual plants up to forest plots. We review the most efficient methods for sampling Hemiptera, for example, beating, pitfall traps, vacuum sampling, intercept traps and chemical knockdown. We examine current knowledge on the response and recovery of Hemiptera to different forest disturbances, such as fire, fragmentation, windthrow, disease and flood. We then illustrate these points by summarizing studies in a forest system being restored following the severe disturbance of mining. Finally, we detail the role that both introduced and native species of Hemiptera display as pests in forest or silvicultural systems, as outbreaks of Hemiptera can indicate when a system is stressed, particularly by drought or flooding.

Keywords: Bioindicators, disturbance, feeding guilds, forest management, insects, pest species, phytophagous invertebrates, true bugs, temporal fluctuations

1. INTRODUCTION

Indicators are components (predominantly biota) of a forest that are measured to provide information about a forest, often for conservation or management purposes (Andersen 1999). Indicator taxa may be adopted for a number of reasons such as determining the success or failure of different forest management practises, for example, burning regimes or selective logging. McGeoch (1998) proposed that indicators be separated into three categories: those detecting environment changes; those detecting ecological changes; or those elucidating the biodiversity within a given system. Environmental indicators detect and monitor changes in the environmental state of the system, ecological indicators can demonstrate the impact of a disturbance in the system, and biodiversity indicators give an indication of an unmeasured part of the diversity of the system. These terms are clearly interrelated; one type of indicator may also display characteristics of another. For example, ecological and environmental indicators may be applicable in studying the recovery of a system after the disturbance of fire.

Over the last 20 years there has been an unprecedented growth in the use of terrestrial invertebrates as ecological indicators as vertebrates have many characteristics that preclude them as suitable indicator taxa (see Hilty and Merenlender 2000). One advantage of invertebrates as indicators, for example, is that many invertebrates are so numerous that repeated sampling of their populations does not usually alter the population dynamics (Williams 1997). Consequently, a wide array of invertebrate taxa are used including ants (Fox 1981; Majer *et al.* 1984; Andersen 1990; Jackson and Fox 1996; Andersen 1997; Griffin 1999; Agosti *et al.* 2000), beetles (Pearson and Juliano 1993; Crisp *et al.* 1998; Oliver *et al.* 1998; Niemelä *et al.* 2000), worms (Abbott 1985; Paoletti 1999), termites (Nichols and Bunn 1980; Davies *et al.* 1999), Collembola (Dindal and Metz 1977; Greenslade and Majer 1993;

Greenslade 1997), grasshoppers (Andersen *et al.* 2001), moths plus butterflies (New 1997; Kitching *et al.* 2000) and spiders (Clausen 1986; Main 1987; Churchill 1997; Brennan *et al.* 2004). Earlier authors often attempted to argue why their particular groups of invertebrate might be superior to other groups. Often such assertions were stated without comparisons with other taxa, and/or research into the validity of the target taxa as indicators (see Andersen 1999). More recently, authors recognise that it is naïve and unrealistic to expect that a single taxon can be used as a predictor for environmental/ecological changes, or biodiversity within a given area (Cranston and Trueman 1997; Azarbayjani and Richardson 1999; Duelli *et al.* 1999; Virolainen *et al.* 2000). Indeed, comparisons between different suites of invertebrates show that different taxa display a variety of responses to the change in environmental conditions (e.g., Lawton *et al.* 1998). Such results promote the use of multiple groups within surveys. Thus, a 'shopping basket' of taxa should be adopted with the inclusion of taxa that will give responses applicable to their different life histories (Niemelä and Baur 1998; Holl and Cairns 2002). This 'shopping basket' may include species with roles as environmental indicators, others as specific ecological indicators, and a further group for the prediction of diversity in the system. This chapter focuses on the potential of Hemiptera as key taxa for inclusion in the shopping basket, a role for which they appear to offer much promise. Indeed, Kitching *et al.* (2001) found hemipteroids (Hemiptera + Thysanoptera = true bugs + thrips), along with ants, most likely to detect site differences across four rainforests separated by latitude.

2. THE POTENTIAL OF HEMIPTERA AS INDICATORS

There are many reasons as to why Hemiptera are potentially excellent ecological or environmental indicators, including: their large contribution to global species diversity; their ubiquitous distribution; high abundances in forest ecosystems; presence at all levels of forest strata; functional importance; wide array of feeding strategies; and their sensitivity to disturbance induced changes in habitat structure, floristics and plant physiology. Below we expand upon these points further.

2.1. Large Contribution to Global Biodiversity

The hyperdiverse order Hemiptera is the fifth most speciose order of insect and the most diverse of all the exopterygote insects (Gaston 1991; Cassis and Gross 1995). One estimate of their diversity suggests 184,000-193,000 terrestrial species globally, excluding all aquatic and semi-aquatic fauna (Hodkinson and Casson 1991). There are over 100 families within three suborders (Heteroptera, Auchenorrhyncha, and Sternorrhyncha), with more families being added continually as their taxonomy is resolved (e.g., Henry 1997; Lis 1999). The abundance and diversity of Hemiptera is demonstrated globally by surveys within all forest systems and strata. For example, in tropical forest canopies, Hemiptera are recorded as the fourth most speciose order after Hymenoptera (wasps, ants, bees), Coleoptera (beetles), and Diptera (flies) (Stork 1991). Within temperate canopies, Hemiptera constitute 9-13% of all species collected from *Eucalyptus* trees, and are the fourth most speciose invertebrate behind Hymenoptera

(19-27% of species collected), Coleoptera (20-25%), and Diptera (11-18%) (Recher *et al.* 1996a). However, in other studies of tree canopies, Hemiptera are often the third most speciose invertebrate order behind the Hymenoptera and Diptera (e.g., Southwood *et al.* 1982). Often Hemiptera are the most speciose herbivore in the canopy, for example, Riberio *et al.* (1998) found hemipteran species composed 56.2% of the total herbivorous fauna (including Coleoptera, Orthoptera, Blattodea and Phasmodea) in a savanna canopy. In the understorey, a highly diverse assemblage of 328 morphospecies from 1,611 individuals of Auchenorrhyncha (leafhoppers, planthoppers, spittlebugs, cicadas) occur in Vietnamese rainforest (Novotny 1993). Moir (2006) records 382 species in the understorey of a temperate Australian forest.

2.2. Ubiquitous Distribution

Hemiptera are abundant on every continent, except Antarctica. They occur in every ecosystem from deserts through to tropical forests, and are also represented by a suite of aquatic or semi-aquatic taxa (e.g., Gerromorpha, Nepomorpha). The earliest ancestral Hemiptera are recorded in the late Moscovian period approximately 307 million years ago (Labandeira 1997). This suggests, Hemiptera, along with cockroaches, dragonflies and crickets, are one of the oldest insect orders, and were abundant by the Permian (250-280 million years ago), prior to the break up of Pangaea. Perhaps this time allowed for the wide diversification into a range of habitats, including cave systems (e.g., Soulier-Perkins 2005). Some individual species are represented on several continents, although the most apparent of these are pest species, particularly of crops (e.g., cereal aphids) and humans (e.g., bedbugs). We return to pest species in Section 6 of this chapter. Others are widespread within single continents (e.g., see Fletcher and Larivière 2001), and provide scope for comparison between areas within a continent. As a whole, however, the ubiquitous distribution of this hyperdiverse order ensures that within any forest system worldwide, Hemiptera are available for use as indicators.

2.3. High Abundance in Forest Ecosystems

Hemiptera are highly abundant in forest systems worldwide. In most arboreal (above the ground) studies, Hemiptera constitute >8% of all invertebrate individuals, or >10% of insect catches within samples. There are many cases in which this figure is reported to be much higher. For example, Schowalter and Zhang (2005) report that herbivorous Hemiptera account for >60% of arthropods on black oak and incense cedar in California. In tropical forest canopies, Hemiptera are recorded as the fourth most abundant order after Hymenoptera (wasps, ants, bees), Coleoptera (beetles), and Diptera (flies) (Stork 1991), although densities of Hemiptera in the understorey of tropical forests are lower (Hodkinson and Casson 1987). Southwood *et al.* (1982) show that of arthropod assemblages on native trees either in England or South Africa, the most abundant species is always a hemipteran. Hemiptera are the third most abundant invertebrate (10% of total catch), after Collembola (42.8%) and Hymenoptera (19.5%), in bark traps on trees in temperate Australian forests (Majer *et al.* 2006). In a study of insect herbivores of a Brazilian savanna, Ribeiro *et al.* (1998) show Hemiptera were the most abundant order (52.4% of total catch) followed by Orthoptera (23.8%), Coleoptera (20%), Blattodea (3.4%) and Phasmodea (0.2%).

At ground level, terrestrial Hemiptera are less abundant than other groups, particularly when compared to Collembola and Acarina, but they still remain in the top ten most abundant invertebrate groups. Further, excluding other invertebrates such as the Collembola and arachnids, Hemiptera are usually in the top four most abundant insect orders. For example, Strehlow *et al.* (2002) found Hemiptera were the seventh most abundant invertebrate and fourth abundant insect order (1.4% of total catch) in pitfall traps from a temperate forest behind Collembola (60.8%), Hymenoptera (19.6%), Diptera (6.1%), Coleoptera (4.7%), Araneae (2.6%), and Acarina (2%). In addition, Fensham (1994) shows that sucking insects constitute 79% of all phytophagous insects collected from woody sprouts in the ground layer of a tropical eucalypt forest.

2.4. Utilize all Levels of Forest Strata

Although best known as plant-dwellers, Hemiptera are not exclusive to this microhabitat, but are present in all forest strata. For example, cicada nymphs, burrowing bugs (Cydnidae) and some mealybugs can be found in the soil feeding on the roots of plants. Many species of Dipsocoroidea hunt other minute invertebrates within the leaf litter. Other Hemiptera, such as Aradidae and nymphs of some Fulgoroidea, inhabit logs or under rocks where they feed on fungi. Several cryptic species are tended underground in ant nests, and feed on roots, or are ‘herded’ out at night by the ants to feed on nearby host plants (e.g., Day and Pullen 1999).

Plant-dwelling Hemiptera occupy a range of microhabitats, and often assemblages within each habitat or strata are unique. For example, a comparison between hemipteran species in the canopy, on bark, in the understorey, and in the soil of a temperate forest in one region of south-west Australia reveals very few species in common (see Postle *et al.* 1991; Heterick *et al.* 2001; Moir *et al.* 2005a,b; Moir 2006). This result is probably partially due to host-specific herbivores targeting a particular plant species. For example, a comparison of canopy and understorey plant species will usually result in significantly different arthropod assemblages (e.g., Claridge and Wilson 1981; Schowalter and Zhang 2005). Furthermore, assemblages of Hemiptera will differ between plant species in just one strata, such as the understorey (e.g., Moir 2006). Moreover, even on a single plant species different species of Hemiptera utilize different microhabitats on an individual plant. Certain Hemiptera are specialised to living and feeding on stems (e.g., Eurymelidae), while others are relatively sedentary on leaves and stems (majority of the Coccoidea), to the extent that some are gall-forming (e.g., some Eriococcidae, Psyllidae and Tingidae). Some species live under bark, while others fly freely between leaves. Other species remain deep within clumps of foliage, such as in grasses, reeds or grasstrees (e.g., Figure 1i, j; Fletcher and Moir 2002). Some herbivorous Hemiptera target flowers or growing shoots due to the high levels of soluble nitrogen present in these regions (Sutton 1984). Predatory species (e.g, Anthocoridae, Reduviidae) may also target flowers as the particular pollinators they attract are favoured prey (see New 1991).

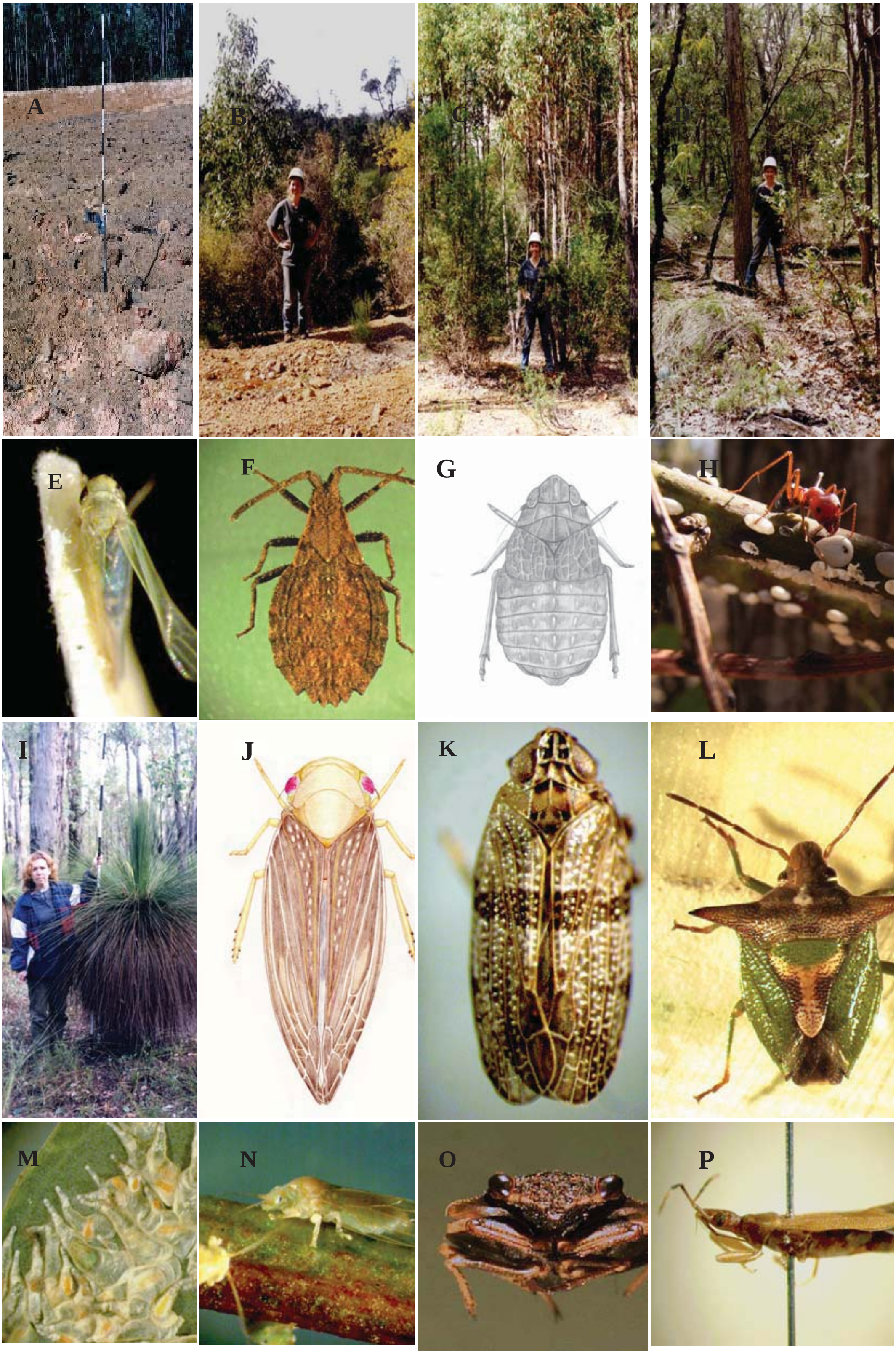
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Figure 1. (a-c) The senior author, M.L. Moir standing in mine pits representing a chronosequence of increasing ages since restoration works up to 9 years post-mining, (d) native unmined jarrah (*Eucalyptus marginata* Sm.) forest, (e) the polyphagous leafhopper *Zygina zealandica* Myers (Cicadellidae) is only ~1 mm in length, (f) the wingless bug *Agriopocoris froggatti* Miller (Coreidae) is often found on *Acacia* species, whereas (g) this wingless undescribed bug (Dictopharidae) is mainly a terrestrial species, (h) ants tending sessile Sternorrhyncha bugs, (i) Australian grasstree *Xanthorrhoea preissii* Endl., (j) grasstree specialist *Cryptobarsac rubriops* Fletcher & Moir (Flatidae), (k) undescribed Achilidae species, the nymphs of which feed on fungi, (l) the stinkbug *Cuspicona longispina* Gross (Pentatomidae), (m) numerous Psyllidae lerps, with each nymph under its own sugary lerp casing, feeding on *Eucalyptus* leaves, (n) Psyllidae adults of the same species (*Glycaspis* sp.) feeding on *Eucalyptus* stems, (o) ground-dwelling predatory toad bug *Nerthra stali* (Montandon), (p) sanguinivorous or blood feeding *Neoclerada westraliensis* Malipatil (Rhyparochromidae).
Photos and drawings: M.L. Moir (e, f, g, j, k, l, m, n, o, p); K.E.C. Brennan (a, b, c, d, i); and J.M. Koch (h).

2.5. High Functional Importance

Being dominant forest insects, Majer *et al.* (2002) suggest that the predominantly herbivorous order Hemiptera are potentially an important indicator group due to their role in nutrient cycling. Casotti and Bradley (1991) found that 0.9 – 1.9 % of leaf area could be lost to herbivores each month in a forest system. Thus, herbivores can increase the rate at which nutrients are recycled in the system by increasing defoliation and providing nutrient-rich frass or insect excrement (e.g., Lamb 1985; Beggs *et al.* 2005; Chapman *et al.* 2003; Frost and Hunter 2004). Hemiptera, in particular, have higher body content of nitrogen than most other insect herbivores, probably due to their method of targeting nutrient-rich sap (Fagan *et al.* 2002). A good example of this is the removal of nitrogen from the soil with the maturation of cicadas, which are below-ground root feeders as nymphs (Table 1). Below-ground systems lost approximately 4 kg N ha^{-1} year^{-1} in grasslands and 1.01 kg N ha^{-1} year^{-1} in forests when cicadas emerge (Callaham *et al.* 2000). Another example of important nutrient recyclers are aphids; they are capable of excreting their body mass in honeydew every hour, or up to 700 kg honeydew ha^{-1} year^{-1} (Stadler *et al.* 2004 and references therein).

Herbivorous hemipteran assemblages are often determined partially by the plant species present (e.g., Moir *et al.* 2005b). However, research has demonstrates that Hemiptera can also regulate the plant communities present by selectively feeding on certain plants and thus reduce plant biomass. Brown *et al.* (1988) show that when herbivores were excluded with insecticide, less diverse, dense swards of grass occurred. They attribute this to the selective feeding on grasses by Auchenorrhyncha (leafhoppers, planthoppers), and Coleoptera (beetles) feeding on short-lived perennials. Furthermore, in some grasslands in the USA, hemipteran species are the most important herbivore (Meyer and Root 1993). Carson and Root (1999) demonstrate that Hemiptera can substantially reduce plant biomass and thus delay plant succession. They suggest that the influence of hemipteran herbivores on plant populations is strongest when the insect population reaches outbreak proportions, or when the herbivore can adequately defend itself against predators that would otherwise keep the population in check. Hemiptera can also influence the plant assemblage through selective seed predation, thereby reducing the germination success of favoured plant species. As mentioned earlier, feeding below-ground on the roots of plants may also affect plant vigour and thus influence aboveground plant assemblages. We detail the importance of Hemiptera as herbivorous pests in Section 6.

Table 1. Examples of taxa representing the different feeding guilds of Hemiptera.

Feeding group	Feeding strategy	Examples
Parasites	Sanguivores/Ectoparasites	Reduviidae[1], Cimicidae, Rhyparochromidae[1] (e.g., *Neoclerada*)
	Kleptoparasites	Miridae of predatory plants[1] (sundew bugs), Berytidae and Reduviidae in spider webs[1].
Predators	Generalists	Gerromorpha[2], Nepomorpha[2], Leptopodomorpha[2].
	Insectivores	Anthocoridae, Nabidae, Reduviidae, Pentatomidae[1] (e.g., *Oechalia*, *Supputius*), Geocoridae.
	Ant/termite specialists	Reduviidae[1] (e.g., *Ptilocnemis*), Miridae[1] (e.g., *Coquillettia*).
	Small prey (e.g., in leaf litter)	Dipsocoroidea, Enicocephalidae.
Omnivores	Both herbivorous (mesophyll feeders) and predatory (insectivores)	Anthocoridae[1], Geocoridae[1], Berytidae, Miridae[1] (e.g., *Campylomma livida* Reuter, *Dicyphus hesperus* Knight, *Lygus hesperus* (Knight))
Herbivores	Root feeders	Cydnidae, Cicadidae[3], Cixiidae[1], Coccoidea[1], Cicadellidae[1].
	Seed feeders	many Lygaeoidea, Cydnidae[1], Pyrrhocoroidea, Pentatomidae[1] (e.g., *Eurygaster*).
	Phloem feeders	Fulgoroidea, Psylloidea, Aphidoidea, Cicadelloidea[4], Cicadellidae[1, 5] (e.g., *Dicranotropis* and *Elymana*), Coccoidea, Aleyrodoidea.
	Xylem feeders	Cercopoidea, Cicadellidae[1, 5] (e.g., *Euscelis, Homalodisca*).
	Mesophyll feeders	Heteroptera[6], Diaspididae, Cicadellidae[1, 5] (e.g., *Zyginidia*).
	Fungivores	Derbidae[7], Achilidae[7], Cixiidae[7], Aradidae.
	Moss/Lichen feeders	Tingidae[1] (e.g., *Carldrakeana* spp.).

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[1] some species only; [2]most aquatic and semi-aquatic families are predacious although some also feed on diatoms, algae, decaying animal or plant material; [3]nymphs only; [4]excluding Cicadellidae; [5]a few Cicadellidae species can switch between xylem, phloem and mesophyll tissue (e.g., *Cicadulina mbila* (Naude)); [6]excluding families mentioned elsewhere; [7]nymphs mycophagous, adults phloem feeders.

As abundant and diverse prey, Hemiptera form important links in most terrestrial food webs and may contribute to the high diversity of other groups. Hemiptera are a food source for many predators (e.g., birds: Tullis *et al.* 1982) and parasites (Waloff and Jervis 1987). Parasite and predator diversity is highly correlated with herbivore diversity (Siemann *et al.* 1998). Hemiptera are also closely tied to other taxa through mutualisms, the best known are associations with ants (Figure 1h). Hemipteran species, predominantly from the families

Aphididae, Cicadellidae, Coccidae, Coreidae, Eriococcidae, Eurymelidae, Margarodidae, Membracidae, Pseudococcidae, Psyllidae and Stitococccidae, support ants by supplying them with honeydew, while the ants protect their 'herd' of bugs from predators (Way 1963; Buckley 1987; Buckley 1990; Buckley and Gullen 1991; Delabie 2001). Through this association with ants, Hemiptera can influence the assemblage of the invertebrate and plant communities within the area (MacKay 1991; Dejean *et al.* 1997; Blüthgen *et al.* 2004). Mutualisms also exist between Hemiptera and carnivorous plants (e.g., *Drosera*), for example, kleptoparasitic Miridae feed on insects trapped by the plant, whilst releasing nutrients to the plant through excretion (China 1953; Ellis and Midgley 1996). Predatory Hemiptera provide a further mutualism by protecting plants from herbivory, which can be more effective than the protection provided by predatory arachnids (see Hodson and Gastreich 2006). Finally, mimicry, such as that of ants by Alydidae and Miridae, is a further interaction (Oliveira 1985; McIver 1987). The purpose of such mimicry is probably to avoid predation, although some predatory Hemiptera use mimicry to deceive ants and feed on ant-tended insects such as aphids (McIver and Stonedahl 1993).

2.6. Wide Array of Feeding Strategies

Although Hemiptera are best known as herbivores, they comprise a wide array of feeding strategies including parasites and predators. Within the herbivores, feeding guilds (*sensu* Root 1967) consist of mesophyll, xylem, phloem, and seed feeders (Figure 2, Table 1). In addition, more primitive families feed on fungi, lichens, mosses or underground roots (Figure 1k e.g., Aradidae, nymphs of Achilidae, Cixiidae and Derbidae are mycophagous – Wilson *et al.* 1994; Cantacaderidae species such as *Carldrakeana tindalei* and *C. pallida* feed on moss and/or lichens – Hacker 1928; Lis 2000). Aside from herbivory, other taxa are predatory (e.g., Reduviidae, Nabidae, Gelastocoridae – Figure 1o), sanguinivorous or blood feeding (e.g., the Rhyparochromidae genus *Neoclerada* Figure 1p, bedbugs of the genus *Cimex*) and omnivorous (e.g., some Berytidae). These guilds and their relationships are outlined in Figure 2 and Table 1, including the variety of herbivorous feeding types. This variety allows assessment of the influence of management practises or disturbances on multiple feeding guilds representing different trophic levels and compartments in terrestrial food webs. Moreover, it allows comparisons of the effects of management practices between areas where there are few or no shared species.

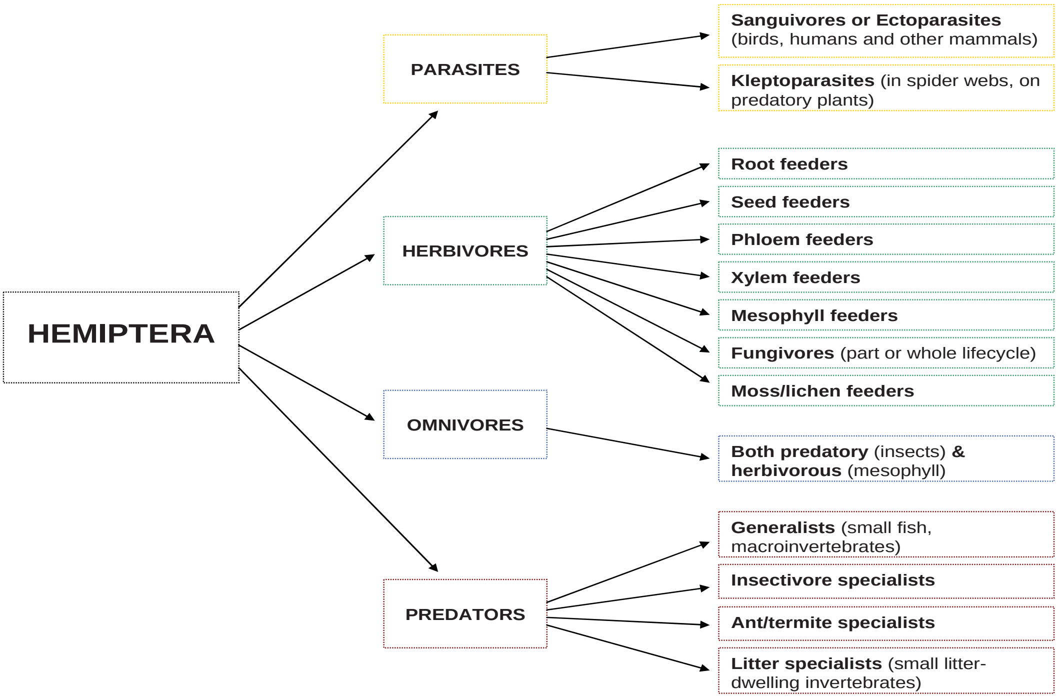

Figure 2. A hierarchical feeding guild classification for the Hemiptera.

2.7. Range of Host-specificity

The most distinguishing feature of Hemiptera is the mode of feeding, which involves extracting plant or animal juices through a proboscis (Carver *et al.* 1991). This has allowed some hemipterans to become more specialised in their feeding habits than their chewing or mining relatives (Hodkinson and Casson 1991; Fensham 1994). Herbivorous species of Hemiptera show a wide degree of host-specificity towards their host-plants. Specificity ranges from those Hemiptera restricted to feeding from a single plant species, genus, or family, to those that are highly polyphagous and can feed on multiple families. Thus, like analyses of feeding strategies, changes in the degree of host-specificity following disturbance can provide additional information to forest managers and like feeding guilds allows direct comparisons between studies where there are no or few species in common. When disturbance removes particular plant species, the resultant hemipteran assemblage may lack bugs host-specific to that plant species (Moir *et al.* 2005b). Moreover, the herbivorous fauna in recently disturbed areas tend to be more polyphagous than in later successional stages, or more permanent habitats (Brown and Southwood 1983; Siemann *et al.* 1999). This can be a response of polyphagous taxa targeting plants higher in nutrients (see Section 6.2 for a discussion of hemipteran outbreaks, and foliar nutrient changes associated with ecological/environmental disturbance). We return to host-specificity in the case study outlined in Section 5.

2.8. Ease of Sampling

Hemiptera are easily sampled using a variety of low cost techniques and adults occur in high abundances, allowing powerful and robust statistical analyses (Southwood 1966; Upton 1991; Moir *et al.* 2005a). We discuss collection methods and sampling protocols for Hemiptera in detail in Section 3.

2.9. Sensitivity to Disturbance

Hemiptera display sensitivity to a variety of disturbances both natural (fire – Siemann *et al.* 1997; drought - Morris and Plant 1983) and anthropogenic (agriculture - Duelli and Obrist 1998; grassland cutting – Morris 1981; grazing – Kruess and Tscharntke 2002; application of fertiliser – Prestidge 1982; chemical spraying - Fauvel 1999; rangeland degradation - Milton and Dean 1992; habitat fragmentation – Ingham and Samways 1996; Hines *et al.* 2005). Moreover, the majority of Hemiptera have short life spans, allowing for fast response to change (Jones 2001). Furthermore, Jana *et al.* (2006) show in a study of the response to pollution in India, Hemiptera are the most sensitive and detrimentally effected when compared to other insect orders (Orthoptera, Hymentoptera, Lepidoptera and Coleoptera). We detail the response of Hemiptera to various forest disturbances and outline their application as indicators in Section 5.

3. SAMPLING PROTOCOLS AND CURATION

In order to use Hemiptera effectively as ecological indicators it is important that careful attention is paid to sampling methods as a wide variety of methods are available and all are biased towards certain taxa (see Upton 1991; Southwood and Henderson 2000). Moreover, all methods differ in their efficiency and, as no study has limitless funds, the most effective methods should be adopted for the particular habitat in question. For example, sweeping may be more efficient in grasslands than chemical knockdown (spraying insecticide and collecting the dead invertebrates which fall to the ground) because the latter disturbs the grass before sampling, resulting in a smaller number of specimens captured per unit of labour expended. However, knockdown is very efficient in tall forest canopies compared to beating, which involves tree climbing.

In addition to biases and efficiencies, to facilitate comparisons between studies it is preferable if established protocols are followed. This is because where comparisons between studies are made, one can never be sure if any differences between studies have arisen merely by the confounding effect of different sampling methods collecting different suites of species. This need for standardised protocols that maximise efficiencies has received much attention in the last decade (see Colwell and Coddington 1995; New 1996; Longino and Colwell 1997; Majer *et al.* 1997). There are now standardised protocols available for many groups of forest invertebrates (e.g., spiders – Coddington *et al.* 1991; ants – Agosti and Alonso 2000; termites - Jones and Eggleton 2000; carabid beetles - Niemela *et al.* 2000), including Hemiptera (Moir *et al.* 2005a). This is important as, although sampling protocols for Hemiptera have long been investigated in agricultural systems (e.g., Biodiversity - Duelli *et al.* 1999; Pseudococcidae – De Barro 1991; Psyllidae – Elder and Mayer 1990; Cicadellidae – Mensah 1996; Delphacidae and Cicadellidae – Perfect *et al.* 1983; Hemiptera – Wilson and Room 1982), the greater structural complexity of forest ecosystems means that these protocols have limited application. Thus in the following sections we consider the results of Moir's *et al.* (2005a) study for sampling Hemiptera in the forest understorey. However, as there is currently no protocols for sampling forest Hemiptera in the overstorey, or at the forest floor, we draw on the agricultural literature where relevant or other general entomological literature.

3.1. Understorey

When assessing different sampling methods for a standardised protocol for Hemiptera, Moir *et al.* (2005a) considered three different understorey structural types arising from different forest management practices; low and open, tall and dense, and an intermediate in structure (Figure 3). Thus even though the study was collected in one forest type, Moir *et al.* (2005a) findings have global application as the habitat structural types they studied are found across many biomes. The sampling methods assessed were sweeping, vacuum sampling, beating, chemical knockdown, branch clipping, hand collecting and sticky trapping. These techniques were tested at two spatial scales: 1 ha sites and individual plants. This is important as ecologists and land managers are often interested at the scale of a forest stand (in which case 1 ha plots are relevant) and sometimes what is occurring on individual plants.

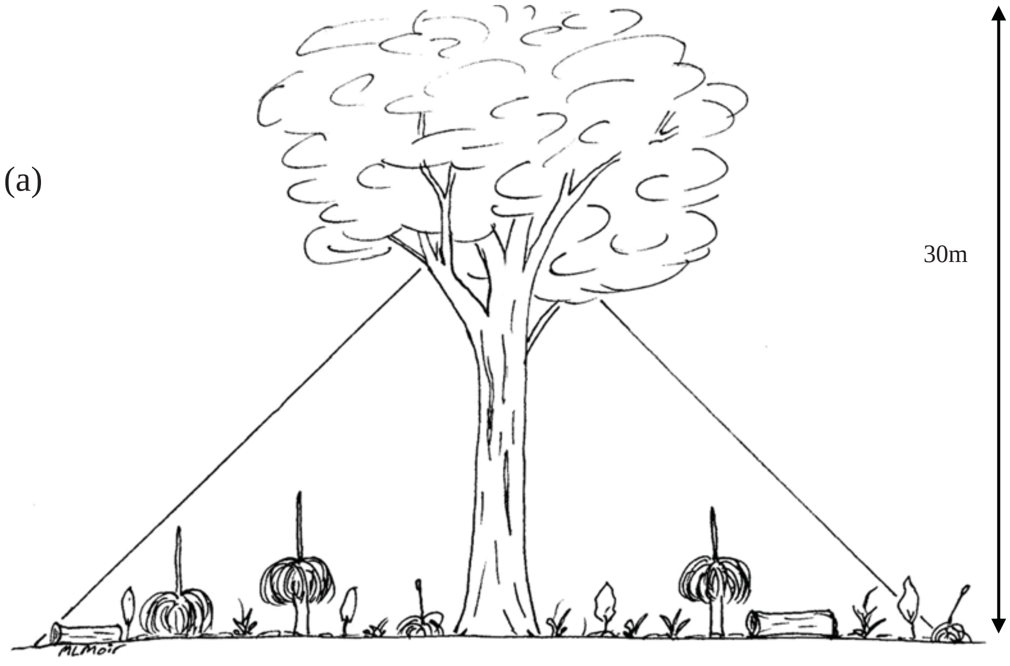

Figure 3. Continued on next page.

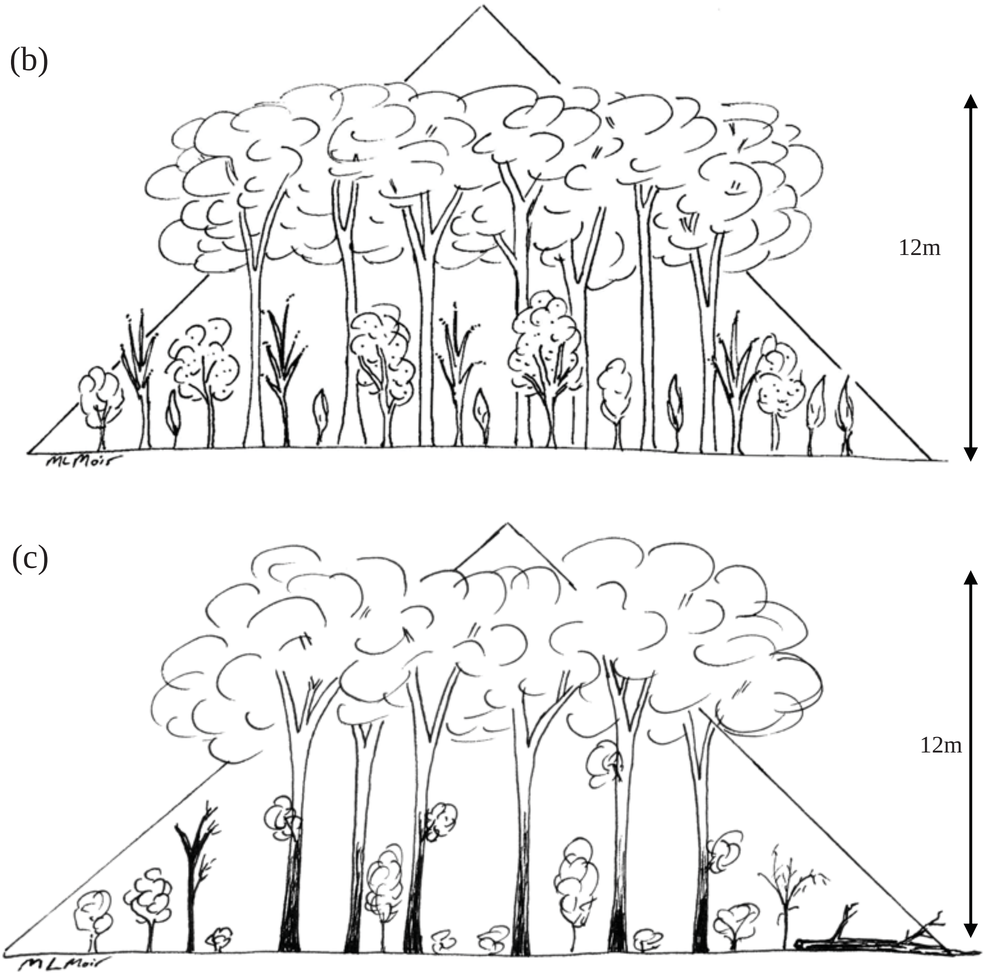

Figure 3. The different habitat structures used by Moir *et al.* (2005a) in which to determine the most efficient and effective sampling techniques for understorey Hemiptera: (a) LOW & OPEN - native jarrah (*Eucalyptus marginata* Sm.) forest, (b) TALL & DENSE - restored bauxite mine pits, and (c) INTERMEDIATE - restored mine pits that have been burnt.

Moir’s *et al.* (2005a) study shows that no single method sampled the majority of hemipteran species in the understorey. The most effective methods to inventory Hemiptera from the understorey are beating and vacuum sampling, as these methods captured high numbers of hemipteran individuals and species, and were relatively time-efficient in the field and laboratory (Moir *et al.* 2005a). If used in combination, these methods optimise the catch of understorey hemipteran species, as each sample has high complementarity (the degree of similarity in species composition between samples of each method). High complementarity is a result of methods targeting different species of fauna allowing more speciose datasets for less units of labour.

3.2. Canopy and Overstorey

For the canopy or overstorey, a number of methods have been developed to increase efficiency of catching a wide suite of invertebrates, particularly in rainforests (see review by Basset *et al.* 1997). Chemical knockdown and branch clipping in combination is adequate for canopy sampling in temperate forest systems (Majer and Recher 1988). Combinations of methods are often required to sample invertebrates with different life-histories, for example, chemical knockdown samples highly mobile invertebrates such as leafhoppers (Cicadellidae, see Figure 1e), while branch clipping targets predominantly sessile fauna such as lerps (Figure 1m), Coccoidea (mealybugs, Figure 1h) and gall-forming fauna. Alternative methods include light traps, bark traps, intercept traps or hand collecting. Light traps (see Southwood 1960; Novotný and Missa 2000), similar to other attractant traps, do not specifically target canopy species, so the origin of the fauna remains unknown. In addition, they are only efficient at night and exclusively sample those species attracted to light (Southwood 1960). Bark traps are effective at capturing invertebrates that utilise the trunks of trees (Majer *et al.* 2003, 2006), as have different intercept traps (Basset 1988; Hill and Cermack 1997; Majer *et al.* 2003, 2006). However, the efficiency and complementarily of these traps in comparison to other sampling methods needs to be examined.

3.3. Forest Floor

For the ground fauna techniques include pitfall traps, extracting Hemiptera from the leaf litter with Tullgren funnels and extraction of Hemiptera from soil cores with Berlese funnels. It should be noted, however, that extraction of litter-dwellers with prior studies show that Tullgren funnels yield few Hemiptera, with much less Auchenorrhyncha and Sternorrhyncha than Heteroptera occurring in samples (Abbott 1984; Postle 1989; Catterall *et al.* 2001). Similarly, the density of Hemiptera in the soil is low. As soil cores collect few Hemiptera, apart from immature scale insects (Abbott 1984; Postle 1989) or mealybugs (De Barro 1991), they appear unwarranted. Despite this, Tullgren funnels and other leaf litter extraction methods are important in obtaining many small, litter-dwelling hemipteran species (e.g., Anthocoridae, Schizopteridae, Ceratocombidae, Dipsocoridae) that are otherwise missing from surveys (Moir unpublished data). In contrast, pitfall traps can yield good abundances of mobile, epigaeic Hemiptera. Pitfall traps are particularly important when surveying Lygaeoidea (seed bugs), Gelastocoridae (toad bugs, Figure 1o), some Tingidae (lacebugs), and brachypterous (wingless) leafhoppers and planthoppers (Figure 1g). They also sample a small proportion of litter-dwelling and soil-dwelling Hemiptera such as Cydnidae (burrowing bugs) and Dipsocoroidea. In addition, some cryptic species, such as fungus-feeding Aradidae are collected in pitfall traps. However, while some plant-dwelling species may fall into the pitfall traps they do not adequately sample invertebrates inhabiting plants and should not be used for this purpose (Majer 1981; Standen 2000). Therefore, it is recommended that when the objective of the project is to sample Hemiptera from a number of different microhabitats within an area, it is critical that pitfall traps be combined with other methods such as vacuum sampling from the understorey, bark traps for the tree trunks and chemical knockdown and/or intercept traps for the canopy (e.g., Schwab *et al.* 2002).

3.4. Curation and Storage

All hemipteran specimens collected require careful curation and storage to permit accurate identification, however, the methods needed depend on the group. Indeed, careful curation preserves specimens for comparison with future studies. Many Heteroptera and Auchenorrhyncha require dry storage by pinning (Figure 1p) or gluing to card (Figure 1e), and are damaged if stored in preservatives such as alcohol. Other groups such as the majority of the Sternorrhyncha (e.g., aphids, mealybugs, plant-lice) require slide mounting for identification. Readers are advised to consult Upton (1991) on the best methods of preservation.

4. TEMPORAL CHANGES IN POPULATIONS

A prominent feature of invertebrate assemblages world-wide are temporal fluctuations resulting in marked changes in population abundances and turnover in species composition. Understanding these temporal shifts is of great importance when using Hemiptera as ecological indicators as temporal differences can sometimes exceed those arising from different forest management practices. The most common temporal changes occur seasonally. Although seasonal fluctuations exist in tropical (Wolda 1980; Novotny 1993) and subtropical (e.g., Basset 1991) systems, changes are most pronounced in temperate regions (e.g., Waloff 1973; Lawton *et al.* 1993; Southwood *et al.* 2004), with some differences between temperate systems of the Southern and Northern Hemisphere. Lawton and Gaston (1989) show phytophage assemblages of English bracken are relatively constant from year to year. Southwood *et al.* (2004) showed that the seasonal turnover in the canopy fauna of English oaks is similarly predictable over five years. In contrast, studies of canopy invertebrates in the Southern Hemisphere shows between-year variations in phytophagous invertebrates can often be greater than seasonal fluctuations (Bell 1985; Recher *et al.* 1996b). Temporal changes in phytophagous invertebrates of the understorey are little studied in the Southern Hemisphere, although one of us has examined the temporal changes in hemipteran assemblages of a Southern Hemisphere forest understorey over 18 months (see Moir 2006). The following case study describes temporal fluctuations of Hemiptera in the understorey of a Southern Hemisphere temperate forest. This work shows the profound importance that a highly abundant species can have on temporal patterns. Such outbreaks of native species may explain (in part) some of the variations of seasonal and annual turnover described earlier between Northern and Southern Hemisphere temperate systems.

Case Study 1: Temporal Fluctuations of Hemiptera in a Temperate Forest of the Southern Hemisphere

Aim

The purpose of this study was to gain background knowledge of the temporal fluctuation in hemipteran assemblages so that they could be used most effectively as ecological of different forest management practices in south-western Australia. Of particular interest was whether sampling in one particular season was indicative of sampling across all seasons and thus act as a surrogate by minimising labour costs.

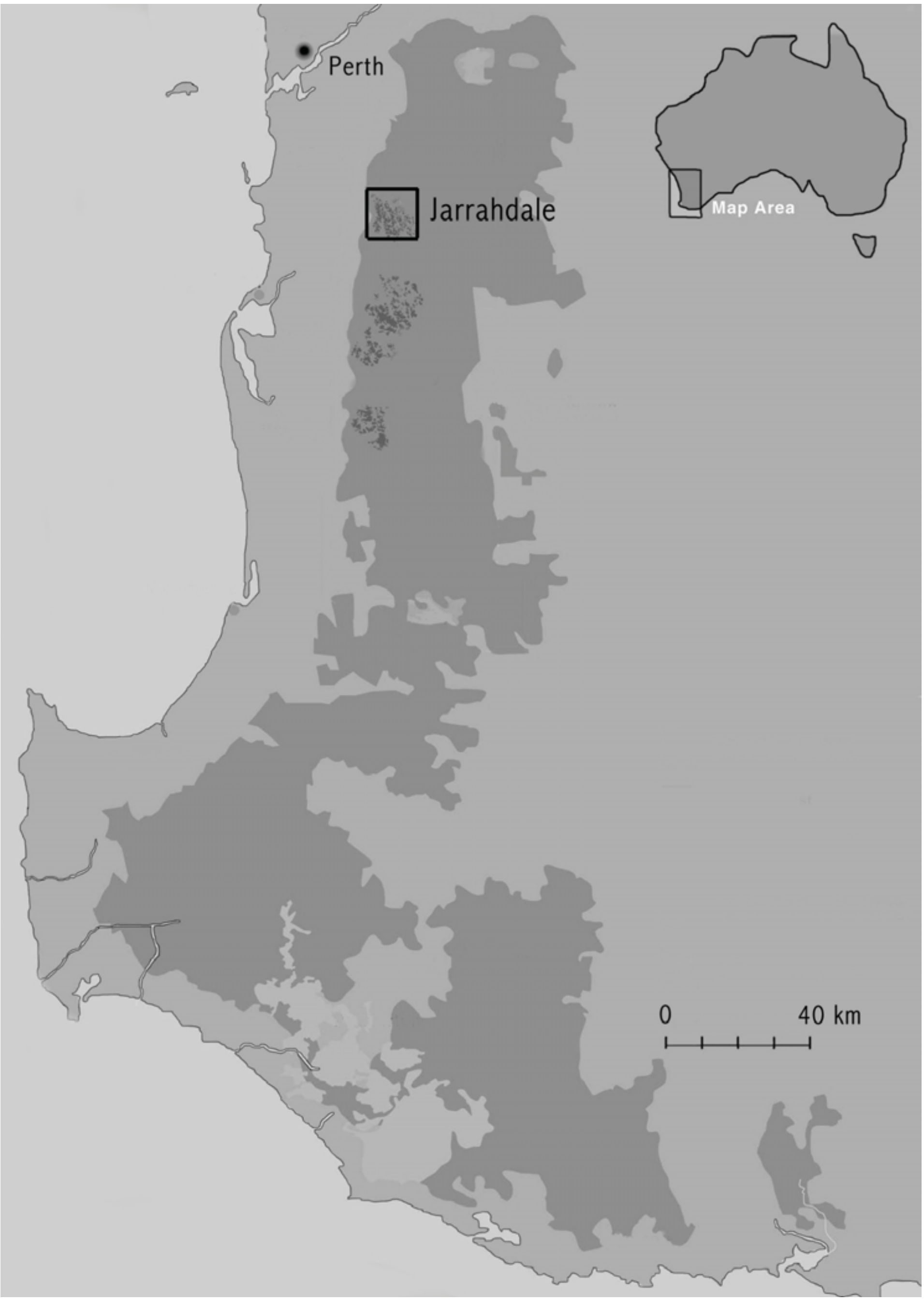

Figure 4. Location of the Alcoa World Alumina Jarrahdale bauxite mine within south-western Australia.

Study Site and Sampling Methods

Hemiptera were sampled for 16 days every season (3 monthly intervals); August 2000 to November 2001 at Jarrahdale, 50 km SE of Perth (32^{o}14'S 116^{o}05'E) in Australia (Figure 4). The temperate jarrah (*Eucalyptus marginata* Sm.) forest has an open structure, with a low understorey dominated by Proteaceae (*Banksia*, *Hakea*, *Grevillea*, *Dryandra*, *Persoonia*), Papilionaceae (*Hovea*, *Chorizema*, *Daviesia*), Xanthorrhoeaceae (*Xanthorrhoea*) and Zamiaceae (*Macrozamia*) (Figure 1d). Sixteen sites were studied with each site having 36 quadrats of 1 x 5 metres, spaced 20 metres apart. In November 2001, the percentage cover of each plant species within all quadrats was recorded. Hemiptera were sampled by vacuuming and beating using the protocol of Moir *et al.* (2005a) (see Section 2 above).

Data Analyses

One-way analysis-of-variance (ANOVA) (type 3 sums-of-squares) tested for differences between sampling period. Dependent variables for ANOVAs were 'hemipteran abundance', 'hemipteran species richness', and '1-Simpson's diversity index'. Dependent variables for ANOVAs were root transformed where Levene's test detected significant departures in homogeneity. F-ratios were considered significant when $P < 0.05$. *Post-hoc* means comparisons used Scheffé's S (Day and Quinn, 1989). Similarity matrices were constructed using the Bray-Curtis measure (Bray and Curtis, 1957) on the abundance of hemipteran species in samples, and the abundance of plant species per quadrat. Root transformation down-weighted the importance of abundant species. Non-metric multi-dimensional scaling (MDS) was performed on the Bray-Curtis matrix (50 restarts) to produce ordinations of similarity in species composition. Analyses of similarities (ANOSIM) (Clarke, 1993) tested for significant differences in species composition between sampling periods. R-statistics were considered significant at $P < 0.05$.

Results

The abundance and richness of hemipteran species differs markedly with sampling period (Table 2). Spring samples have significantly more individuals and species than most others (Figure 5a,b). Higher abundance in Spring 2000 however, is attributable to an outbreak of the Cicadellidae species *Zygina zealandica* (Figure 1e). When *Z. zealandica* is removed, abundance in Spring 2000 is similar to other periods (Figure 5c). The outbreak of *Z. zealandica* may also account for lower diversity in Spring 2000 (Figure 5d).

Table 2. F-ratios from one-way ANOVAs of differences in Hemiptera between sampling periods

Dependent variables	Sampling period $df_{5, 72}$
Hemipteran abundance	12.525***
Hemipteran abundance (less *Zygina zealandica*)	4.271**
Hemipteran species richness	25.185***
Hemipteran diversity (1-Simpson index)	4.334**

** denotes P<0.01, *** denotes P<0.001.

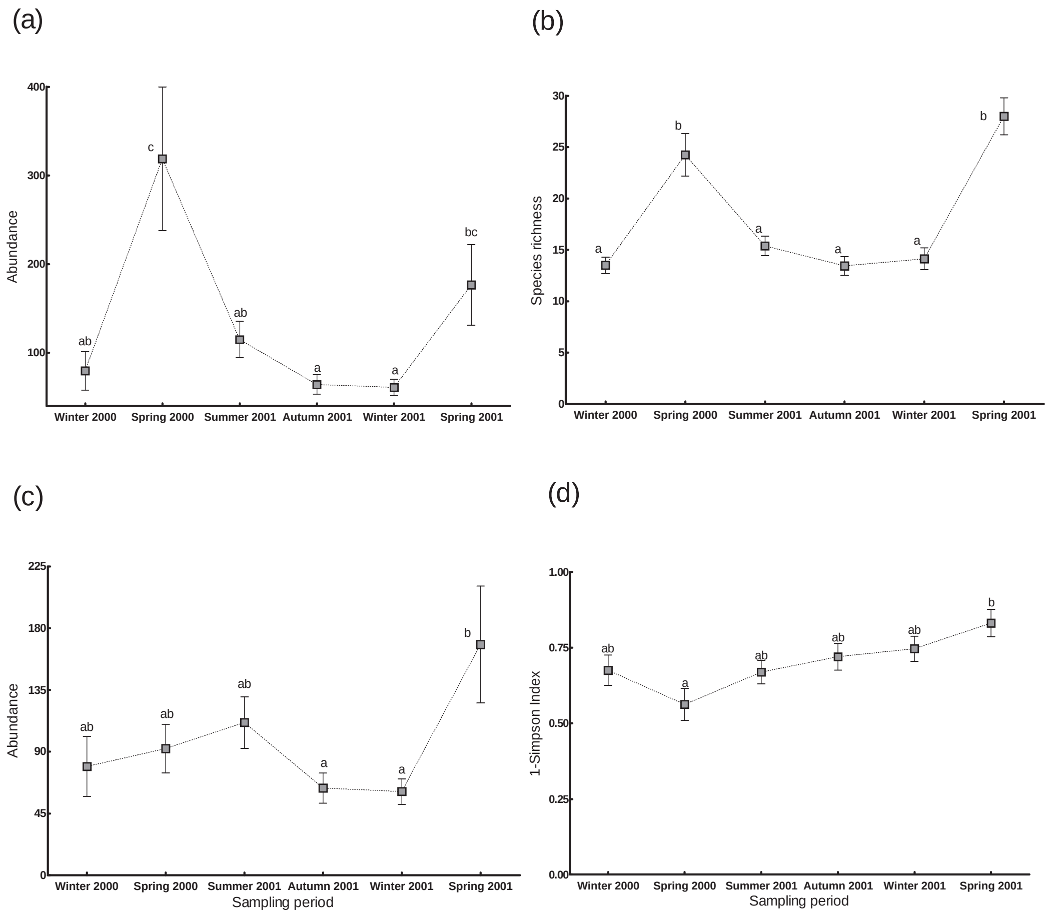

Figure 5. Significance from *post-hoc* tests of ANOVAs (means with different letters are significantly different from each other at P < 0.05) for (a) total abundance, (b) species richness, (c) abundance without *Zygina zealandica*, and (d) 1-Simpson diversity index plotted against sampling periods (standard error bars are shown).

In terms of species composition, hemipteran assemblages follow a distinct seasonal pathway, with significant differences in species composition between sampling periods (Figure 6, Table 3). Interestingly, despite following a cyclic pattern, seasons sampled twice (*i.e.*, spring and winter) differ significantly between years (Table 3).

Table 3. R-statistics and significant levels of pair-wise differences in hemipteran species composition from one-way ANOSIMs between sampling periods (Global R = 0.548*)**

	Winter 2000	Spring 2000	Summer 2001	Autumn 2001	Winter 2001
Spring 2000	0.731***				
Summer 2001	0.485***	0.654***			
Autumn 2001	0.232***	0.691***	0.259***		
Winter 2001	0.241***	0.808***	0.533***	0.175**	
Spring 2001	0.789***	0.724***	0.633***	0.644***	0.702***

** denotes P<0.01, *** denotes P<0.001.

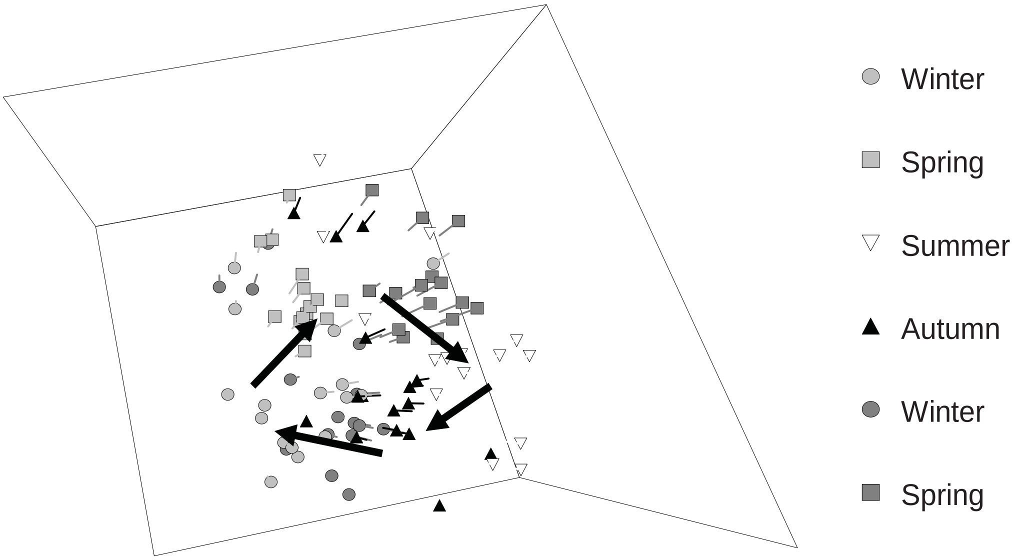

Figure 6. Ordination of hemipteran species composition in each of the six sampling periods within the understorey of an Australian temperate forest. Samples closer to each other have higher similarity in species composition.

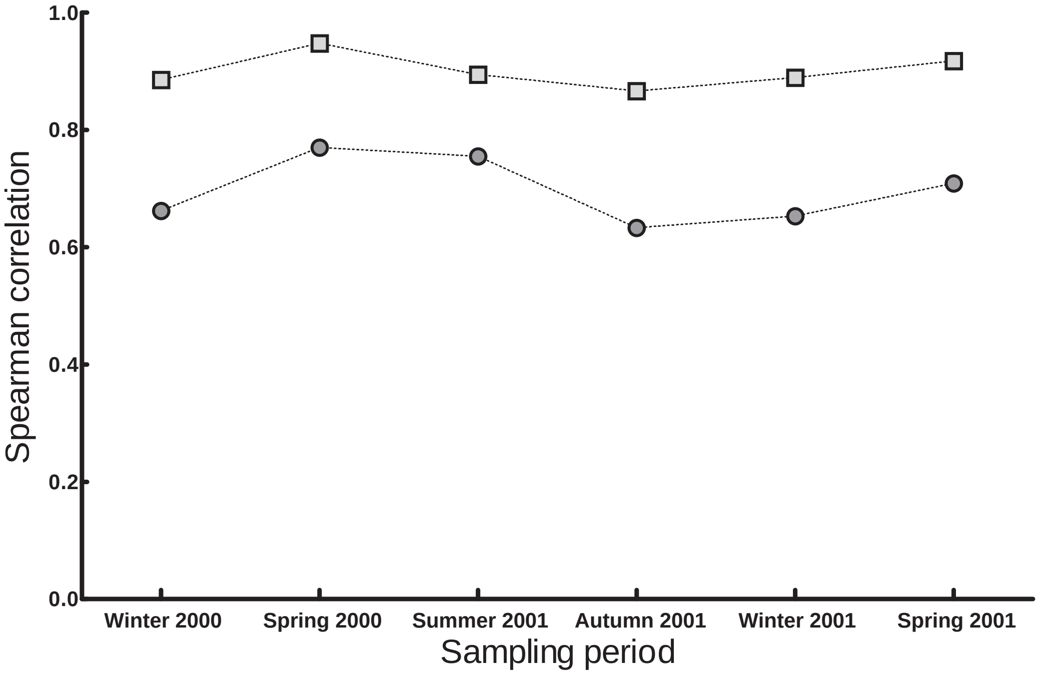

Figure 7. Similarity in hemipteran species composition within a single season compared to the overall assemblage pooled across all seasons (squares) Also shown in the similarity of the hemipteran species composition in each season compared to plant species composition (circles).

Despite the hemipteran assemblages following a seasonal trajectory, the degree of congruence of each sampling period to the overall assemblage (when the data was pooled across all sampling periods) was relatively constant (R^2 (season) = 0.866 to 0.948), with a minor strengthening of the relationship in Spring 2000 (Figure 7). Interestingly, the degree of congruence of Hemiptera with the plant assemblage showed much greater variation with sampling period. Congruence between Hemipteran and plant species composition was strongest in Spring 2000 plus Summer 2001, and weakest in Autumn 2001 (Figure 7).

Discussion

This research shows significant yearly fluctuations of hemipteran populations in the understorey, and confirms findings documented for phytophagous invertebrate assemblages in Southern Hemisphere temperate overstoreys (e.g., Bell 1985; Recher *et al.* 1996b). These yearly fluctuations ensured that hemipteran assemblages on understorey plants in this system were not predictable. But despite sampling years with and without a strong El Niño event, resulting in drought for 2001 (Bureau of Meteorology, unpublished data), fluctuations in hemipteran abundance, species richness and composition were greater between seasons than between years. This differed from the overstorey in which fluctuations were greater between years than between seasons (Bell 1985; Recher *et al.* 1996b).

Despite marked shifts in hemipteran species composition between sampling periods, the results of this study suggests that if logistics limit the duration of the sampling to just one season, sampling in spring is a good surrogate of what might be collected over an entire year. Moreover, during spring, hemipteran assemblages are most similar to plant composition at this time, thereby reflecting host-specificity and other plant relationships more accurately. We note, however, that other authors have recorded peaks in species richness and abundance of Hemiptera in south-western Australia also during summer (Majer 1981; Postle 1989) and autumn (Worsley Alumina Pty Ltd. 1999). Differences between the studies may be explained by differences in sampling protocol, vegetation, location, climatic conditions and target taxa. Thus, despite the encouraging surrogacy results presented here, it is prudent for all studies, regardless of their global location, to collect for more than one season (Cranston and Trueman 1997). This is especially important in temperate regions (Lawton *et al.* 1993). Other authors have noted that insect populations can change anywhere from 10- to 100-fold between generations (Strong *et al.* 1984). Given this, the study of such populations must be analysed with caution and multiple sampling years are strongly recommended. In this study, the occurrence of a very abundant species (*Zygina zealandica* (Myers)) in one year emphasises the need for sampling over multiple years, as such species can markedly alter perceptions of abundance and species diversity.

5. RESPONSE TO DISTURBANCE

As noted earlier in Section 2, Hemiptera are sensitive to disturbances that fragment or alter forest structure or floristics, as well as disturbances that alter plant physiology and chemistry. Disturbances that fragment or alter forest structure and floristics may include timber harvesting, prescribed burning or wildfires, mining and urbanization, windthrow and hurricanes. These disturbances, along with droughts and floods may also alter plant physiology and chemistry. The few studies investigating the response of Hemiptera to these disturbances show Hemiptera are one of the most adversely affected arthropod orders by forest fragmentation (Ingham and Samways 1996) and logging (Strelow *et al.* 2004). By contrast, however, windthrow and the restoration of logged areas can increase the abundance and species richness of some Hemiptera, which presumably respond to an increase in leaf production (Neumann 1991; Basset *et al.* 2001). In response to fire, the species richness and abundance of Hemiptera decrease more significantly than most other invertebrates in the year following burning (Siemann *et al.* 1997; Andersen and Muller 2000). This result is presumably due to the initial mortality of animals by the fire or mass exodus from the area by those with good dispersal powers, as has been documented for stink bugs immediately after burning (Gillon 1971) and other taxa such as spiders (Brennan *et al.* 2006). However, frequent burning regimes can increase the overall abundance of Hemiptera in forest systems (York 1999). These apparently paradoxical results may be explained by the long association that invertebrates can have with fire in fire-prone systems such as some prairies (Evans 1984), tropical savannah (Andersen and Muller 2000; Andersen *et al.* 2005) and temperate forests (Moir *et al.* in press). This long association has enabled invertebrates to survive the fire in refugia or quickly recolonise from unburnt areas. Although we emphasis that those species particularly vulnerable to such disturbances will be restricted in their dispersal and thus may have difficulty in recolonising. Such taxa include small litter-dwelling Hemiptera (e.g., Dipsocoroidea) or species with reduced wings, termed brachypters (see Figure 1f,g), and we consider the latter more closely in Case Study 2. We note here, however, that when these species can utilise refugia throughout such disturbances as burning, then their populations may be less detrimentally affected. For example, refuges from fire is provided by logs, rocks and burrows within the soil for terrestrial invertebrates (Andrew *et al.* 2000; Brennan *et al.* 2004) and particular plants for plant-dwelling arthropods (e.g., grasstrees of Australia – Moir *et al.* in press, Figure 1i; zamia palms – Dolva and Scott 1982; bunch grasses of North America - Riechert and Reeder 1972).

There is scant information on Hemiptera in primary succession, although there are many studies following secondary disturbances, particularly in grassland systems (e.g., fire – Morris 1975, grassland regimes – Southwood *et al.* 1979; Brown *et al.* 1988; Morris 1990a; Huusela-Veistola and Vasarainen 2000; Nickel and Achtziger 2005). The most rigorous studies of Hemiptera undertaken during any succession have a Northern Hemisphere bias, with few studies in the tropics or Southern Hemisphere (although see Ingham and Samways 1996). Moreover, the majority of studies have targeted the suborders Auchenorrhyncha (leafhoppers, planthoppers, cicadas, spittle-bugs - Figure 1e,g,j,k) and/or Heteroptera (stink-bugs, assassin bugs, lace-bugs, plant-bugs, toad-bugs, seed-bugs - Figure 1f,l,o,p) but omit the Sternorrhyncha (mealybugs, aphids, plant-lice, scales - Figure 1h,m,n). This paucity of information is surprising considering their diversity and importance. Most species of Sternorrhyncha are phytophages and many are monophagous (feeding from a single plant species or plant genus). Because of this, hemipteran assemblages are sensitive to changes in the richness and species composition of plant communities (e.g., plant species diversity, plant species composition and structural complexity). The case study below outlines the return of plant-dwelling Hemiptera during restoration following mining, and concentrates on the role that dispersal ability and the plant assemblage plays in the resulting hemipteran assemblages.

Case Study 2: Restoration of Forest Hemipteran Assemblages Following Bauxite Mining

Alcoa World Alumina Australia mines bauxite in the southwest of Australia, and restoring mined pits back to a native forest ecosystem is a desired goal following mining. A full description of Alcoa's mining and restoration procedures can be found in Gardner (2001). Consequently, returning not just the plants but also the invertebrates is important to ensure that the biodiversity values of the forest are maintained. As Hemiptera have close associations with plant species, their recolonisation has been of special interest to land managers as some of the plant species in the forest are very difficult to re-instate following mining. Determining the role of Hemiptera in mining succession complements studies of invertebrate taxa that have been conducted in relation to bauxite mine restoration and the surrounding native jarrah forest (see Majer *et al.* in press). With the exception of Casotti and Bradley (1991), who focused on the effects of herbivory on the dominant overstorey species of *Eucalyptus*, surveys of invertebrate herbivores and recolonisation following mining are scant.

Moir *et al.* (2005b) examined hemipteran recolonisation along a chronosequence of mine pits where restoration works had been applied 4 years, 6 years and 9 years previously (Figure 1a-c), and contrasted this with the assemblages present in surrounding unmined jarrah forest (Figure 1d). The disturbance of mining and subsequent land denudation is somewhat comparable to a primary succession for fauna, as all individuals must recolonise from outside the disturbed site. Although, unlike true primary succession, topsoil from areas of forest being cleared for mining are transported to pits where restoration works are taking place. It is noteworthy also that this study was based on an unusually large data set for Hemiptera within succession (at least three times the number of specimens than most other data sets); notable exceptions are the secondary succession data sets of Morris (1990b) and Siemann *et al.* (1999). In this context, this paper is a major contribution to knowledge of recolonisation by invertebrates during succession.

The results of Moir *et al.* (2005b) show that the overall plant and hemipteran assemblages of all successional stages after restoration were not the same as assemblages from native forest (Moir *et al.* 2005b). The richness of plant species remained at a plateau throughout all successional stages, which was below that found in unmined forest. In contrast, some structural attributes of the vegetation in pits became more similar to the forest with time, for example, the density of live vegetation 80 to 300 cm in height declined from younger to older pits to become more similar to forest sites. Plant species composition changed with time but was not tracking directly towards compositions found in unmined forest. The abundance and richness of hemipteran species of all successional stages remained at similar values to those in the forest. In terms of species composition, the Hemiptera were following the same trajectory as the vegetation, and with greater time were not expected to reach compositions similar to that found in unmined forest. These findings show land managers, therefore, that if they want to re-establish hemipteran assemblages in restored pits similar to that in unmined forest, greater attention is needed in getting the plant assemblages and vegetation structure in restored mine pits to more closely resemble that in the unmined forest.

Brachypterous fauna were used by Moir *et al.* (2005b) to analyse the role of dispersal capability in the recolonisation of Hemiptera as this may dictate when a species appears in the succession. Brachypterous fauna have lower dispersal capability than other hemipteran species as they tend to walk or jump rather than fly (see Socha and Zemek 2003) (Figure 1f,g). In contrast, other wingless taxa, such as the Coccoidea (mealy bugs, lerps and scale), utilise alternative dispersal methods, such as transportation by tending ants (Way 1963; see Figure h) or dispersal as aerial plankton (Barrass *et al.* 1994). Moir *et al.* (2005b) found that recolonisation by brachypterous Hemiptera (with permanently reduced wings) was markedly slower than for winged taxa or Coccoidea fauna. However, by 9 years after restoration the brachypterous fauna was recolonising and was not significantly different from the forest fauna.

Feeding mode was also analysed by Moir *at al.* (2005b) as herbivorous species of Hemiptera may follow a different trajectory after mining than the predatory species due to differences in their lifecycles. They found that while the majority of the herbivorous fauna were following the trajectory of the plant assemblages over time, predatory Hemiptera were not on a similar trajectory to the plant assemblages, and may have been more influenced by vegetation structure. Also of importance was the observation that the early stages of succession were characterised by a high abundance of generalist hemipteran species whereas specialist taxa were more characteristic of later successional stages.

6. OUTBREAKS OF OVER ABUNDANT SPECIES AND HEMIPTERA AS FOREST PESTS

Hemipteran species are major pests in agricultural, plantation and native forest systems due to their ability to disperse quickly and breed to very large populations in short periods of time. Therefore, their inclusion in surveys is essential when the purpose of the study is to determine the effect of forest disturbance and management. Large population changes of hemipteran species can signify a forest system under stress and intervention or alteration of management practises. Furthermore, exotic hemipteran species can often invade natural systems, especially if they have a wide host range. Early identification of such species, and their associated parasites, may be essential to preserve the native fauna and flora.

Worldwide, the most detrimental hemipteran pests of forests are species of Psyllidae (plant-louse), Aphididae (aphids), Coccoidea (scale, mealybugs), Coreidae (fruit-spotting bugs, crusader bug, gumtree bugs), Lygaeidae (seed bugs, Rutherglen bug – *Nysius vinitor* Bergroth) and some Pentatomidae (stink bugs). In the following section we outline the information that can be gained from studying these Hemiptera.

6.1. Hemiptera as Pests in Agricultural Crops and Plantations

Although some Hemiptera may have poor dispersal abilities making colonisation difficult, other species have particularly good powers of dispersal enabling them to quickly locate regions and plants with abundant food resources. Such species can become pests if unlimited by food resources, predation/parasitism or unfavourable environmental conditions. Excellent examples are aphids on cereal crops (e.g., De Barro 1992) and mealybugs in citrus orchards (e.g., Beattie *et al.* 1990). Other hemipteran species are problematic not just because their feeding causes defoliation, wilting or stunted plant growth, but because of viruses that the bug unwittingly transports may also result in plant damage. Examples, of viruses dispersed by hemipterans are aphids spreading sugar cane mosaic virus (Noone *et. al.* 1994) and the Glassy Winged Sharp-Shooter (*Homalodisca coagulate*: Cicadellidae) spreading Pierce's disease in grapevines, which has threatened California’s wine industry.

Often introduced plant species, such as those in plantations and crops, have distinct pest species. However, native or introduced hemipteran species are able to become new pests of crops and plantations when they are able to feed on a wide range of host plants. For example, the Glassy Winged Sharp-Shooter, is highly polyphagous and is, therefore, not only a pest of grapevines in the USA, but also citrus, plums and soybeans, to name a few (Andersen *et al.* 2003). Another example, the Australian Rutherglen bug has a very wide host plant range, and consequently is a pest of agriculture, turf and eucalypt plantations (Carver *et al.* 1991; Strauss 2001). Alternatively, a relatively host-specific insect pest may be accidentally introduced to a new region with their host. The bluegum plant-louse (*Ctenarytaina eucalypti* (Maskell): Psyllidae) is a native to the eastern states of Australia but has become a pest species of *Eucalyptus* plantations in New Zealand, Western Australia, California and Chile (Lanfranco and Dungey 2001; Strauss 2001; Withers 2001). In fact, highly host-specific Hemiptera accidentally introduced from Australia comprise the largest proportion of all specialist pests within New Zealand eucalypt plantations (Withers 2001). Herbivores are likely to become pests in monoculture systems because the system has greater predictability and homogeneity than native systems, and may provide conditions for increased survival and reproduction (Jones 2001). In addition, host plants are easier to locate in monocultures (Tahvanainen and Root 1972) and there are fewer natural enemies, especially generalist predators (Andow 1991; Steinbauer *et al.* 2001).

6.2. Hemipteran Outbreaks in Forests

Hemipteran outbreaks can also occur in native forests, as we noted with the outbreak of the leafhopper *Zygina zealandica* in Section 3 (*Temporal and Annual Changes in Populations*). Similar situations as in crops or plantations usually cause outbreaks of these Hemiptera in forests; unlimited food resources and/or favourable environmental factors. However, unlike in crops or plantations, low predator and parasitoid abundance is not often the cause of outbreaks as they occur naturally in native systems. In agricultural and plantation systems, indiscriminate insecticide use can eliminate the insect predators. Also, introduced herbivore pests may not have their associated predators or parasites present in the region. Within native systems, semiochemicals (chemical signals) released by the feeding of herbivores on their host can attract predators and parasitoids (Price 1997). Herbivore populations are thus naturally managed by increases in predators, parasites and/or disease when at high densities. When this situation is altered, such as the removal of predators and parasites by insectivorous birds, outbreaks of herbivores occur causing serious damage to the host plant (e.g., Stone 1996). Yukawa (1984) documented large outbreaks of the scale *Crypticerya jacobsoni* (Green) (Margarodidae) covering one island, Rakata Besar, in the Krakatau Islands. He attributed the outbreak to the simplified nature of the island’s ecosystem, with a lack of scale predators and parasitoids. Host plants themselves can induce chemical resistance at the event of herbivore outbreaks, often termed *induced defense hypothesis* (see Price 1997 for a full explanation and examples), although this form of herbivore control may be less effective than other mechanisms such as predation and parasitism (Kaitaniemi *et al.* 1999).

In terms of biomass, food resources do not change in native systems as rapidly as the establishment of a new crop or plantation. However, after some forest disturbances such as fire, the flush of new plant growth may cause a greater abundance of herbivores (e.g., York 1999 – Hemiptera in pitfall traps; Andersen and Müller 2000 – crickets, beetles and Homoptera in sweep samples; Radho-Toly *et al.* 2001 – Hemiptera and beetles in chemical knockdown samples). Following a fire, plants may experience flushes of nutrients, which may encourage population growth in insect herbivores (Radho-Toly *et al.* 2001). Thus, environmental conditions are interrelated with food resources and can promote herbivore outbreaks. Some environmental conditions are adverse for the host plant, which induces stress and increases the concentration of nutrients in the sap (White 1984), the food of herbivorous Hemiptera. For example, Bell (1985) documented outbreaks of scale on *Exocarpos* and *Jacksonia* plants in savanna woodland within the first year of a drought, although populations crashed after the drought continued into a second year. In tree plantations, Stone (2001) noted that controlling induced plant stress caused by flooding, weed competition and drought reduced the levels of herbivory, although she did not measure the abundance of herbivores. In contrast, rises in atmospheric carbon dioxide associated with climate change causes a decrease in sap nitrogen concentration, and thus, reduces populations of herbivores (Watt *et al.* 1995).

In native systems the population of insect herbivores is often regulated by density-dependent factors (Elliot *et al.* 1996). The occurrence of predators, parasitoids, and incidence of disease usually increase as the herbivore population increases. Plant defences may alter with higher densities of herbivores. In addition, at higher densities, birth rates decline, death rates increase and dispersal is promoted in the herbivore population (e.g., Denno *et al.* 1986). Outbreaks of native herbivores can be considered keystone species in forest management as, at outbreak levels, the insect can regulate and reduce stands of host plant species (Carson *et al.* 2004).

7. CONCLUSION

Hemiptera are prime candidates as ecological or environmental indicators of forest systems. They are one of the most diverse and abundant orders of invertebrate within forest systems worldwide. Due to their high abundance in forests, they play a key role in nutrient cycling and link between trophic levels in forest food webs. Hemiptera have close associations with plants, and although herbivorous assemblages are predominantly regulated by plant composition, they in turn can regulate the plant composition by selective herbivory. The crucial role Hemiptera play in both plant regulation and nutrient cycling is accentuated when they attain outbreak numbers. Hemipteran populations are heavily influenced by temporal variation, particularly in temperate regions. Sampling in multiple seasons and years shows that outbreaks of native species in forests can be short-lived, but can alter the perception of diversity for that sampling period and can indicate changed ecological or environmental conditions. Hemiptera provide a wide range of feeding guilds and host-specificity levels in which to analyse the response of taxa with different ecological requirements to disturbance and management practises in forests. Thus Hemiptera are important taxa for the indicator ‘shopping basket’. Furthermore, as with all invertebrate orders, care must be taken to use the most effective and appropriate sampling protocol (mix of sampling methods) to collect taxa. Thus, we conclude by arguing that given their diversity, abundance, ubiquitous distribution, presence at all levels of forest strata, functional importance, variety of feeding guilds, wide spectrum of host-specificity levels, and sensitivity to disturbance Hemiptera are excellent ecological and environmental indicators. In particular, Hemiptera are useful in providing early forecasts of whether forest management practices are sustainable.

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Chapter 5

EFFECT OF PARENT MATERIAL AND PEDOGENIC PROCESSES ON THE DISTRIBUTION, FORM AND DYNAMICS OF ORGANIC CARBON IN FOREST ECOSYSTEMS IN NW SPAIN. A BIOGEOCHEMICAL APPROACH

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ABSTRACT

The main objective of the present study was to determine the effect of the type of pedogenesis generated by two different parent materials – amphibolite (AMP) and granite (GR) - and the effect of different forest stands - pine (P), eucalypt (E), and oak (O) – on the quality and quantity of organic C pools in udic, mesic and freely drained systems. Five C pools were studied: aboveground biomass, belowground biomass, dead wood, litter, and soil organic matter (SOM) in the Ah horizons. The three forest soils derived from AMP materials (AMP-P, AMP-E, AMP-O) were classified as Typic Fulvudands and Aluandic Andosols, and the three forest soils derived from GR rocks (GR-P, GR-E, GR-O) were classified as Humic Dystrudepts, and Leptic and Haplic Umbrisols. All soils are located in the surroundings of Santiago de Compostela (A Coruña, NW Spain), where the mean annual air temperature is 12.3 ºC and the total annual precipitation is 1624 mm yr^{-1}. The results obtained indicate that highest total organic C stocks in the ecosystems studied (down to the lowest depth of the Ah horizons), i.e., the sum of the five reservoirs considered, always corresponded to the eucalypt stands, with stocks > 500 t ha^{-1}, whereas those of the oak and pine stands were always < 500 t ha^{-1}. The mean distribution of organic C stocks in the five reservoirs considered was as follows: aboveground biomass, 18.4%; belowground biomass 4.6%; dead wood, 1.1%; litter 8.4%; and soil organic C, 67.2%; there were no significant differences ($P < 0.05\%$) between means of the AMP and GR ecosystems although the total C stocks were always higher in the AMP than in the GR ecosystems, and followed the order E > P > O in both. There were significant differences ($P<0.05$) in the quantity, quality and dynamics of organic C in the two types of ecosystems, when organic layers (L and F) and also Ah horizons (Ah1 and Ah2) were distinguished, as discussed below.

The results indicate that, in soils developed from GR, the lithology mainly determines the type of pedogenesis taking place in the surface horizons, with intense acidification (acid-complexolysis) associated with scarce or nil neoformation of secondary minerals in the most acidic compartments (L and F layers) and an abundance of aqueous and mobile organo-metal complexes. Under such conditions, decomposition of primary OM is very slow, leading to the accumulation of undecomposed debris in the organic layers. In soils developed from AMP, both lithology and plant species clearly affected pedogenesis in the surface horizons. Surface acidification occurred in the pine stand (although never as intense as that occurring on GR materials), but greater than that of AMP-E and AMP-O litters. In general, the more eutrophic conditions of the AMP soils, compared with the GR soils, appeared to allow rapid decomposition of primary OM. The geochemical conditions of the AMP Ah horizons also appeared to allow neoformation of metastable forms of gibbsite and different short-range order 1:1 aluminosilicates able to bind to secondary organic compounds. Under such conditions, decomposition of secondary OM was probably preserved, as reflected by the high organic C content of the Ah horizons. All of this may explain the existence of a moder-type OM in the GR soils, in comparison with the Al-mull type form of the AMP soils. Overall, the results obtained indicate that parent material affects the distribution within the soil profiles studied, as well as on its quality and dynamics within the soil profiles studied, whereas the organic C stocks present in the aboveground biomass were more affected by the type of forest species and management.

INTRODUCTION

Organic matter (OM) has multiple effects on soil properties as it is involved in chemical, physical, and biological processes. Loss of OM affects the capacity of soils to sustain crop growth, enhances the risk of soil erosion and decreases soil biodiversity; mineralization of OM contributes negatively to the global climate change by increasing levels of atmospheric CO_2. Soil OM thus performs many functions vital to life, which explains the importance attached to it in international conventions on Desertification, Biodiversity, and Climate Change. Until the 1970s, increasing levels of atmospheric CO_2 were mainly attributed to agricultural practices, rather than to industrial and transportation activities (Lal, 2001). Currently agricultural practices still represent around 20% of global anthropogenic greenhouse gas emissions, with soils being an important source of the emissions (Lokupitiya & Paustian, 2006). This provides an idea of the magnitude of the organic C losses from agronomic soils (which in soils from Galicia, NW Spain, range between 30 and 50%), and manifests the urgent need to revert this trend and promote soils as a C sink. However, in order to enhance organic C accumulation in soils in a sustainable and efficient way, management practices that result in the build up of organic C in soils and favour organic C stability must be encouraged. This demands (i) fundamental insights into the mechanisms of organic C stabilization in soils, which are still not well understood, and (ii) advanced knowledge of the ultimate potential of soils to accumulate organic C, which to date is still uncertain (Lützow et al., 2006). In a recent review of the mechanisms that are currently considered to contribute to OM stabilization in temperate soils, Lützow et al. (2006) defined stability as the integrated effect of (i) selective preservation (referred to as the relative accumulation of recalcitrant compounds), (ii) spatial inaccessibility, and (iii) interaction with surfaces and metal ions. The latter authors indicated that the major difficulties encountered in making advances in this area originate from the simultaneous occurrence of different stabilization processes.

The C accounting system to be used during the first commitment period (2008-2012) of the Kyoto Protocol, as described in the Good Practice Guidance for Land Use, Land-Use Change and Forestry (LULUCF) (IPCC, 2003), does not distinguish between OM characteristics, and only total organic C is considered. However, in the guidance, different types of soils are distinguished: (i) soils containing highly active clays, (ii) soils containing poorly active clays, (iii) sandy soils, (iv) spodic soils, (v) volcanic soils, and (vi) wetland soils. Thus, the existence of soils that differ in their ability to stabilize OM is implicitly recognized in the guidance, with the lithology being the most important factor in this type of soil grouping, although other soil forming factors, such as time, climate and drainage conditions, also exert effects. Parent material may directly affect OM stability by (i) surface chemistry and organo-mineral interactions (McKeague et al., 1986; Macías & Chesworth, 1992), which also change, along with mineral evolution, during pedogenesis (Chorover et al., 2004), and (ii) the effect that particle size has on particle aggregation.

Parent material also has an indirect effect on OM stability through the weathering rate and base cation release, which affect soil fertility and reactivity, and through effects on soil drainage and root architecture, all of which, in turn, affect aboveground and belowground biological activity. Thus, the lithology has many, probably concominant, effects on the different OM stabilization mechanisms. In the present study biogeochemical analyses were carried out (i) to discern the extent to which the type of pedogenesis generated by amphibolite and granite materials in freely drained systems affect the organic C quality and quantity in different forest systems - pine, eucalypt, and oak – grown under the same climatic conditions, and (ii) to elucidate whether this affects the C cycle in these ecosystems.

MATERIALS AND METHODS

Site Description

The sampling sites were in Monte Pedroso and Boqueixon, both of which are close to Santiago de Compostela (A Coruña, Spain). The mean annual air temperature in Santiago de Compostela (altitude 260 m) is 12.3 ºC, and total annual precipitation is 1624 mm yr^{-1}. The lithology of Monte Pedroso consists of a granitic massif, and that of Boqueixon of a metabasic amphibolitic massif. The dominant minerals in the former are quartz, microcline, acid plagioclases, muscovite and biotite, whereas in the latter minerals such as amphiboles (mainly hornblende) and plagioclases predominate (Macías et al., 1982). Three forest sites –

each consisting of different species (pine, eucalypt, and oak stands, respectively) - and a crop site, in which corn was cultivated, were studied on each type of parent material. The sampling and the field study were carried out in spring 2006. The three forest soils derived from amphibolite (AMP) rocks (AMP-P, AMP-E, AMP-O) were classified as Typic Fulvudands (Soil Survey Staff, 1999) and Aluandic Andosols (IUSS Working Group WRB, 2006), and the three forest soils derived from granite (GR) rocks (GR-P, GR-E, GR-O) were classified as Humic Dystrudepts (Soil Survey Staff, 1999) and Leptic and Haplic Umbrisols (IUSS Working Group WRB, 2006). The cultivated soils derived from AMP (AMP-C)and GR rocks (GR-C) were classified as Oxic Dystrudept and Humic Distrudept (Soil Survey Staff, 1 999), respectively, and Ferralic Cambisol and Cambic Umbrisol (IUSS Working Group WRB, 2006), respectively (Table 1).

Table 1. Site description

Site code	Site	Parent material	Vegetation	Approx. Trees Age	Soil Taxonomy (1999)	IUSS WRB (2006)	UTM coordinates
AMP-P	Boqueixon	Amphibolite	*Pinus pinaster* Ait.	35	Lithic Hapludand	Aluandic Andosol	29T 544231 4743446
AMP-E	Boqueixon	Amphibolite	*Eucalyptus globulus* Labill.	10	Lithic Hapludand	Aluandic Andosol	29T 543605 4745373
AMP-O	Boqueixon	Amphibolite	*Quercus robur* L.	40	Lithic Hapludand	Aluandic Andosol	29T 544259 4743920
GR-P	Pedroso	Granite	*Pinus pinaster* Ait.	25	Typic Dystrudept	Leptic Umbrisol	29T 535292 4748760
GR-E	Pedroso	Granite	*Eucalyptus globulus* Labill.	18	Typic Dystrudept	Leptic Umbrisol	29T 535333 4748224
GR-O	Pedroso	Granite	*Quercus robur* L.	30	Typic Dystrudept	Haplic Umbrisol	29T 534376 4751691
AMP-C	Boqueixon	Amphibolite	corn	-	Oxic Dystrudept	Ferralic Cambisol	29T 543747 4742070
GR-C	Pedroso	Granite	corn	-	Humic Dystrudept	Cambic Umbrisol	29T 534001 4751582

In the two pine stands (*Pinus pinaster* Ait.) (AMP-P and GR-P) studied, the understory basically consists of *Pteridium aquilinum* (L.), Kuhn and *Ulex* sp., and some ericaceous species. In the granite site (GR-P), there are also some saplings of *Acacia melanoxylon* R. Br., whereas in the amphibolite site (AMP-P) there are some eucalypts (*Eucaliptus globulus* Labill.), probably because of the presence of eucalypt plantations in the surrounding area. Both eucalypt plantations (AMP-E and GR-E) show a high presence of *Ulex* sp. in their understory. There is a noteworthy presence of *Erica arborea* L. on amphibolites (AMP-E), whereas on granites (GR-E), ferns (*Ptridium aquilinum* L.), *Calluna* sp. and grasses were also present. There is a very dense coppice in the oak stand on amphibolites (AMP-O), and the forest floor is covered with *Hedera helix* L., with no understory. Together with the main species (*Quercus robur* L.) there are other species such as *Betula sp.*, *Castanea sativa* Mill. and *Laurus nobilis* L. There are also some *Pinus pinaster* Ait. and eucalypt saplings in the oak stand on granite site (GR-O). The understory mainly consists of *Ulex* sp., heathers (*Calluna* sp; *Erica* sp.), and *Pteridium aquilinum* (L.) Kuhn; *Frangula alnus* Miller is also present.

For the quantification of total organic C present in each forest site, the IPPC Good Practice Guidance for LULUCF (2003) was followed (except for measuring the soil depth). The guidelines define five organic C pools: (i) litter, (ii) SOM, (iii) aboveground biomass, (iv) belowground biomass, and (v) dead wood, which – according to the Marrakech Accords (UNFCCC, 2001) - should all be accounted during the first commitment period (2008-2012) unless a country chooses “not to account for a given pool, if transparent and verifiable information is provided that the pool is not a source.” Thus, for sampling and biomass estimation, the former pools were considered, as described below.

LITTER AND SOIL ORGANIC MATTER

Sampling of Litter and Soil Organic Matter

According to the IPPC guidance, “litter includes all non-living biomass of a diameter less than a minimum diameter chosen by the country (for example 10 cm), in various states of decomposition above the mineral or organic soil.” This includes the layer containing fresh leaves (L), the decaying layer of fragmented leaves (F), and the humified layer (H). In the present study a diameter of 10 cm was chosen. The same guidance defines “soil organic C” as that present “in mineral and organic soils (including peat) to a specified depth chosen by the country and applied consistently through a time series”. The use of a standard depth of soil (e.g., 0-30 cm at Tier 1 level) for all soil types in different land cover uses is proposed. However, in this study soil samples were taken from the lower depth of the Ah horizons, which varied in the forest soils studied from 40 to 50 cm depth (Table 2). The depth of the Ap horizons in the cultivated soils was 25 cm. To estimate the organic C lost due to changes in land use (e.g., forestry to agriculture), comparisons were made on the basis of equal soil mass rather than on the basis of equal depth, as recommended by Ellert & Bettany (1995) and Post et al. (2001).

Table 2. Values of several physicochemical properties of the different litter samples

Hor.	Sample code	Depth	pH-H_2O	pH-ClK	pH-NaF	Al_p	Fe_p	C_p	Al_p/C_p	$(Al_p+Fe_p)/C_p$
		(cm)				(g kg^{-1})			(mol mol^{-1})	
L	AMP-P	6-3	4.70	4.13	6.69					
	AMP-E	6-3	4.83	4.43	6.97					
	AMP-O	6-3	4.83	4.55	6.84					
	GR-P	4-3	3.41	2.77	6.29					
	GR-E	6-3	3.93	3.50	6.19					
	GR-O	6-3	4.41	3.96	6.36					
	AMP†		4.79a	4.37a	6.83a					
	GR†		3.92b	3.41b	6.28b					
F	AMP-P	3-0	4.15	3.42	7.98	18.20	10.54	134.3	0.06	0.08
	AMP-E	3-0	4.91	3.69	7.70	1.88	1.58	64.4	0.01	0.02
	AMP-O	3-0	4.93	4.20	8.41	8.98	6.34	84.9	0.05	0.06
	GR-P	3-0	3.78	2.68	6.30	1.49	1.29	49.0	0.01	0.02
	GR-E	3-0	3.83	2.76	6.39	5.37	3.03	96.5	0.03	0.03
	GR-O	3-0	3.59	2.60	6.44	4.99	4.59	75.3	0.03	0.04
	AMP†		4.66a	3.77a	8.03a	9.68a	6.16a	94.5a	0.04a	0.05a
	GR†		3.73b	2.68b	6.38b	3.95a	2.97a	73.6a	0.02a	0.03a

† Mean values of each variable studied within AMP and GR rows followed by the same letter are not significantly different at the 0.05 level of probability.

At each forest site, soil cores were collected manually from soil pits, and the L and F layers, and the Ah1 and Ah2 horizons were distinguished. For laboratory analyses, a bulk sample was collected by removing approximately 1 kg of soil from each horizon sampled. For bulk density, soil cores of a known volume were collected from each horizon, and the dried soil (48 h at 105ºC) was weighed. For microbial analyses, subsamples were stored at <4ºC (for approximately 2 wk) until determinations were carried out. For chemical analysis of mineral soil samples, the samples were air-dried, sieved to 2 mm, and stored at room temperature. For chemical determinations of the L and F layers, the corresponding samples were oven-dried at 65º C for 24 h and then stored at room temperature.

General Chemical and Physical Characterization of Litter and Soil Organic Matter

The pH was measured in H_2O and in KCl using a 1:2.5 soil:solution ratio (except for the L and F layers for which a 1:5 soil:solution ratio was used). The pH in NaF at 2 min (Fieldes & Perrot, 1966) was also measured to identify either reactive Al or the presence of free organic acids. Organic C content and total N were analyzed by combustion with a LECO analyzer (Model TruSpec CHN, LECO Corp., St Joseph, MI). Sodium pyrophosphate (Bascomb, 1968) extractable Al, Fe, and C (Al_p, Fe_p, and C_p) were measured in each soil sample. Carbon in the sodium pyrophosphate extract was determined using a spectrophotometer for the UV-vis spectrum (Model UVIKON 930 Kontron Instruments), whereas Al_p and Fe_p were determined by atomic absorption spectrophotometry (Perkin-Elmer 2380, Norwalk, CT). The major elemental composition of all samples was determined after acid digestion (6:2.5; HNO_3:HCl ratio), except that of Si, which was determined after digestion with a mixture of HNO_3, HF, and HCl concentrated acids (9:4:1 ratio) and later addition of boric acid to neutralize excess HF. Total Ca, Mg, Al, Si, and Fe were determined by atomic absorption spectrophotometry, Na and K by atomic emission spectrophotometry (Perkin-Elmer 2380, Norwalk, CT). The equilibrium solution was obtained in an aqueous suspension (1:10 soil:solution ratio) that was allowed to equilibrate for three days. Thereafter, pH and electrical conductivity (EC) were measured, and solutions were filtered through a 0.45 μm filter. Dissolved Al was determined by colorimetry with pyrocatechol violet (Dougan & Wilson, 1974). Total F was determined by use of an ion selective electrode with a Methrohm 692 meter (Methrohm Ldt, Herisau, Switzerland) and TISAB II-Orion decomplexing solution. Dissolved Ca, Mg, Al, Si, Fe, Na, NH_4, and K were determined by ion chromatography (Model Dionex-4500i, Dionex Corp., Sunnyvale, CA), and dissolved organic C (DOC) using a FLOWSYS Third Generation Continuous Flow Analyzer (Systea, Anagni, Italy). Chloride, SO_4, NO_3, and PO_4 were determined with the same chromatograph. Species activities were calculated from the chemical data obtained from the equilibrium solution using the Solmineq88 program (Kharaka et al., 1989). A geochemical model of mineral stability was constructed (Chesworth, 2000) for the SiO_2-Al_2O_3-H_2O, by making use of the different chemical species used by Chesworth & Macías (2004). Finally, soil texture was determined by laser diffractrometry (Model Mastersize 2000 with a high dispersion unit, Hydro MU, Malvern Instruments Ltd., UK).

Chemical and Biological Characterization of the Main Carbon Pools in Litter and Soil Organic Matter

Hot-water extractable C (HWC) was determined in moist field samples of the L layers following the method of Ghani et al. (2003). The extraction consists of a two-sequence step procedure involving the removal of readily soluble C from the litter followed by the extraction of labile components of soil C at 80ºC for 16 h. Dissolved organic C in both extracts was determined with a FLOWSYS Third Generation Continuous Flow Analyzer (Systea, Anagni, Italy). Microbial biomass C (C_{mic}) was determined in field moist samples of the L and F layers following the procedure of Vance et al. (1987). Duplicate sub-samples (3 g dry weight) were fumigated with chloroform for 24 h and then extracted with 0.5 M K_2SO_4 for 2 h on an end-over-end shaker. The suspended samples were centrifuged and filtered through Whatman 42 filter paper. Similar sets of non-fumigated samples were extracted in the same way. The amount of total C in the extracts of the fumigated and non-fumigated samples was determined with a spectrophotometer at 445 nm for the UV-vis spectrum (Model UVIKON 930 Kontron Instruments). The C flush values were used as the indicator C_{mic}.

The oxidability of soil organic C by $KMnO_4$ (MnoxC) was determined with 33 mM $KMnO_4$ after 1 h incubation (Tirol-Padre & Ladha, 2004). Samples, each containing the equivalent of 15 mg of organic C (calculated from the known total C content of each layer studied), were added to centrifuge tubes. Twenty five mL of 33 mM $KMnO_4$ were dispensed into each centrifuge tube and the same volume of $KMnO_4$ was also dispensed into empty centrifuge tubes to serve as blanks. The tubes were capped and covered with aluminium foil before shaking for 1 h on a reciprocal shaker. Samples were centrifuged at *1030 x g* for 5 min. Two mL aliquots of $KMnO_4$ from each sample and blank were transferred into 50-mL volumetric flasks and diluted to the final volume. The absorbance of the samples and blanks was then measured at 565 nm with a UVIKON 930 spectrophotometer (Kontron Instruments, Milan, Italy). The concentration of $KMnO_4$ in the samples and blanks was determined by use of a standard calibration curve. The amount of MnoxC in the sample was computed considering that C is oxidized from the neutral state (0) to C^{+4}, and that $Mn^{+7}O_4^-$ is reduced to $Mn^{+4}O_2$ (Tirol-Padre & Ladha, 2004; Clapp et al., 2005), and was expressed as the percentage of MnoxC in the total organic C of that fraction (MnoxC*100/SOC).

Basal respiration was measured with a Micro-Oxymax Respirometer (Columbus Instruments, Columbus, OH). The instrument includes gas sensors for continuous measurement of changes in the concentrations of O_2 and CO_2 in the head space of reaction vessels. Each vessel (250 mL volume) was filled with undisturbed field moist samples (20 g for the F layers and Ah horizons, and 10 g for the L layers), and connected to a closed circuit. Basal respiration was measured during 24 h. The metabolic quotient, qCO_2 (μCO_2-C mg biomass-C h^{-1}) was estimated by taking the hourly rate of basal respiration and dividing it by the estimated microbial biomass C. Finally, neutral (NDF) and acid (ADF) detergent fibres and acid detergent lignin (ADL) were determined following the fibre analysis of Van Soest and Robertson (1985). Neutral detergent fibre mainly contains cellulose, hemicellulose, and lignin, whereas ADF contains cellulose and lignin. The ADF fraction was further analyzed to determine the ADL, with 72% (v/v) H_2SO_4.

Estimation of Aboveground Biomass, Belowground Biomass, and Dead Wood

According to the IPPC Guidance (2003), aboveground biomass is defined as “all living biomass above the soil including stem, stumps, branches, bark, seeds, and foliage”; belowground biomass is defined as “all living biomass of live roots. Fine roots of less than 2 mm diameter (suggested) are often excluded because these often cannot be distinguished empirically from soil organic matter or litter”; finally, dead wood is defined as “all non-living woody biomass not contained in the litter, either standing, lying on the ground, or in the soil”.

The standing biomass was estimated in the selected stands in a randomly located transect, 50 m long and 6 m wide. As the stands are small, this transect was usually large enough to cross the entire stand. A measuring tape was placed on the floor and the diameter at breast height (DBH; 1.3 m) of all standing trees, alive or dead, inside the transect area was measured. The height of at least the three trees with the largest DBH, three trees with the lowest DBH and three trees with average DBH was measured. The height of all trees of different species of the dominant tree and of all standing dead trees (snags) was also measured. Allometric equations developed for the studied species in Spain were used to estimate standing tree biomass (Montero et al., 2005). In the same transect and at both sides of the measuring tape, three randomly selected 2 x 2 m squares were destructively cut to the ground to estimate the understory biomass. The samples were transported to the laboratory, dried at 60ºC until constant weight for at least one week and weighed. The biomass present in the dead wood (> 0.4 cm) lying on the forest floor was estimated by the line intersect sampling protocol (Ringvall & Ståhl, 1999) and the wood volume (m^3 ha^{-1}) was estimated by equation [1] (Marshall et al 2003) applying the wood densities of the studied species found in the region (Miguel Ángel Balboa, pers. comm). All the dead wood was assumed to be fresh, and therefore of a similar density to that of the live trees.

$$v_i = \frac{\pi^2}{8 \times L} \sum_{j=1}^{m_i} d_{ij}^2 \tag{1}$$

In equation [1], V is the wood volume, d the diameter of the piece of dead wood intersecting the transect, and L the transect length. Finally, belowground biomass was calculated taking into account the default values given by the IPCC (2003), which vary depending on type of species and aboveground biomass.

RESULTS AND DISCUSSION

Litter

Chemical Characterization of Litter

The mean pH-H_2O values of the AMP L and F layers were significantly higher ($P < 0.05$) than the corresponding means of the GR L and F layers (L layers: 4.79 compared with 3.92, and F layers: 4.66 compared with 3.73, respectively) (Table 2); those of the AMP organic layers were in the pH range of acid-hydrolysis and were thus mainly controlled by dissolved CO_2, and those of organic GR layers were in the pH range of acid-complexolysis, whereby a combination of acid hydrolysis and complexolysis takes place (Pedro & Sieffermann, 1979), and is thus mainly controlled by free organic acids. The pH-NaF values should indicate, to a certain extent, the presence of free organic acids in the system. The aim of this test is mainly to identify reactive Al surface, in the presence of which the F anion should react and release OH^- to the solution (Mizota & Wada, 1980), causing an increase in the solution pH from its initial value of ~7.8. However, when organic acids are abundant, they may cause a decrease in the initial pH of the solution, even in the presence of reactive Al (Perrot et al., 1976), and thus this measure is a qualitative indicator of the presence of free organic acids when the pH of the soil suspension in NaF is lower than that of the NaF solution. Mean pH-NaF values of the L and F layers of the AMP soils were significantly higher ($P < 0.05$) than those of the L and F layers of the GR soils (L layers: 6.83 compared with 6.28; F layers: 8.03 compared with 6.38, respectively) (Table 2), thus confirming the greater presence of free organic acids in the GR systems. In a study of the same GR and AMP forest systems, Camps Arbestain et al. (2003) detected free organic acids, such as oxalic acid, in the GR Ah1 horizons, at pH-H_2O values < 4.4, although not in AMP Ah1 horizons, all of which had pH-H_2O values > 4.4.

Table 3. Values of pH and EC of the solutions after they were allowed to equilibrate for three days, and values of ionic strength, log (aAl^{3+}/aH^{3}), $pSiO_4H_4$, and pSO_4, estimated by the Solmineq88 program (Kharaka et al., 1989)

	Layer/ horiz.	pH	EC	Al	Ionic strength ($x10^{-4}$)	Log (aAl^{+3}/aH^{3})	$pSiO_4H_4$	pSO_4	Termo-dynamic groups†
			μS cm^{-1}	mg L^{-1}					
AMP-P	L	4.5	234	0.17	1	7.5	3.7	3.5	II
	F	4.6	105	1.31	6	8.9	4.0	4.2	III
	Ah1	4.5	43	0.13	3	7.7	4.0	4.2	II
	Ah2	4.5	56	0.22	4	8.1	4.1	3.9	II
AMP-E	L	4.8	329	0.26	25	8.7	4.0	3.2	III
	F	5.3	98	0.98	4	10.5	4.7	4.4	IV
	Ah1	5.1	36	0.49	2	9.7	4.2	4.4	IV
	Ah2	5.6	38	0.28	2	10.3	4.3	4.3	IV
AMP-O	L	5.0	345	0.34	20	9.4	3.7	5.0	IV
	F	5.7	120	1.03	5	11.1	4.0	4.3	IV
	Ah1	4.6	28	0.32	2	8.6	4.3	4.4	III
	Ah2	5.4	26	0.11	2	9.6	4.3	4.3	IV
GR-P	L	4.2	154	0.17	4	6.5	4.1	4.1	I
	F	4.1	100	0.09	5	5.9	4.0	4.3	I
	Ah1	4.5	24	0.51	2	8.5	4.7	4.5	III
	Ah2	4.8	15	0.15	1	8.7	4.7	4.6	III
GR-E	L	4.3	233	0.17	20	6.9	4.0	4.3	II
	F	4.5	79	0.07	3	6.7	3.7	4.6	II
	Ah1	4.8	17	0.26	1	9.0	4.5	4.6	III
	Ah2	4.8	14	0.13	1	8.5	4.5	4.5	III
GR-O	L	4.5	543	0.18	20	7.7	3.5	3.9	II
	F	4.2	104	0.47	4	7.7	4.0	4.5	II
	Ah1	4.7	19	0.24	1	8.7	4.5	4.6	III
	Ah2	5.1	19	0.14	1	9.2	4.5	4.5	III

† Group I: None of the minerals is stable. Concentration of Al controlled by organo-Al complexes. Strong acid-complexolysis.

Group II: Kaolinite stable, gibbsite unstable. Concentration of Al controlled by organo-Al complexes and kaolinite. Moderate acid-complexolysis.

Group III: Kaolinite stable, gibbsite saturation. Concentration of Al by gibbsite of different degrees of crystallinites. Acidolysis.

Group IV: Kaolinite stable, gibbsite and allophane saturation. Concentration of Al controlled by microcrystalline gibbsite. Andic character. Moderate acidolysis.

The solution equilibrium data (Figure 1) indicates that the L and F layers of the soils studied corresponded to three out of the four situations encountered. The L and F layers of the GR soils under pine were included in group I, which corresponds to a highly acidic system, in which there is no stable mineral, except quartz. The pH of both equilibrium systems was ≤ 4.2 (Table 3), concentrations of organic acids were high (as estimated from the pH-NaF values) (Table 2), and the Al saturation was very low (log (Al^{3+} + 3pH) ≤ 6.5) (Figure 1; Table 4), i.e.

considerably lower than that needed for the stability of either kaolinite or gibbsite. Under these conditions neither pedogenic Al hydroxides nor Al silicates are thermodynamically stable (Skyllberg, 2001) and Al solubility is likely to be controlled by complexation with OM (Gustafsson et al., 2001).

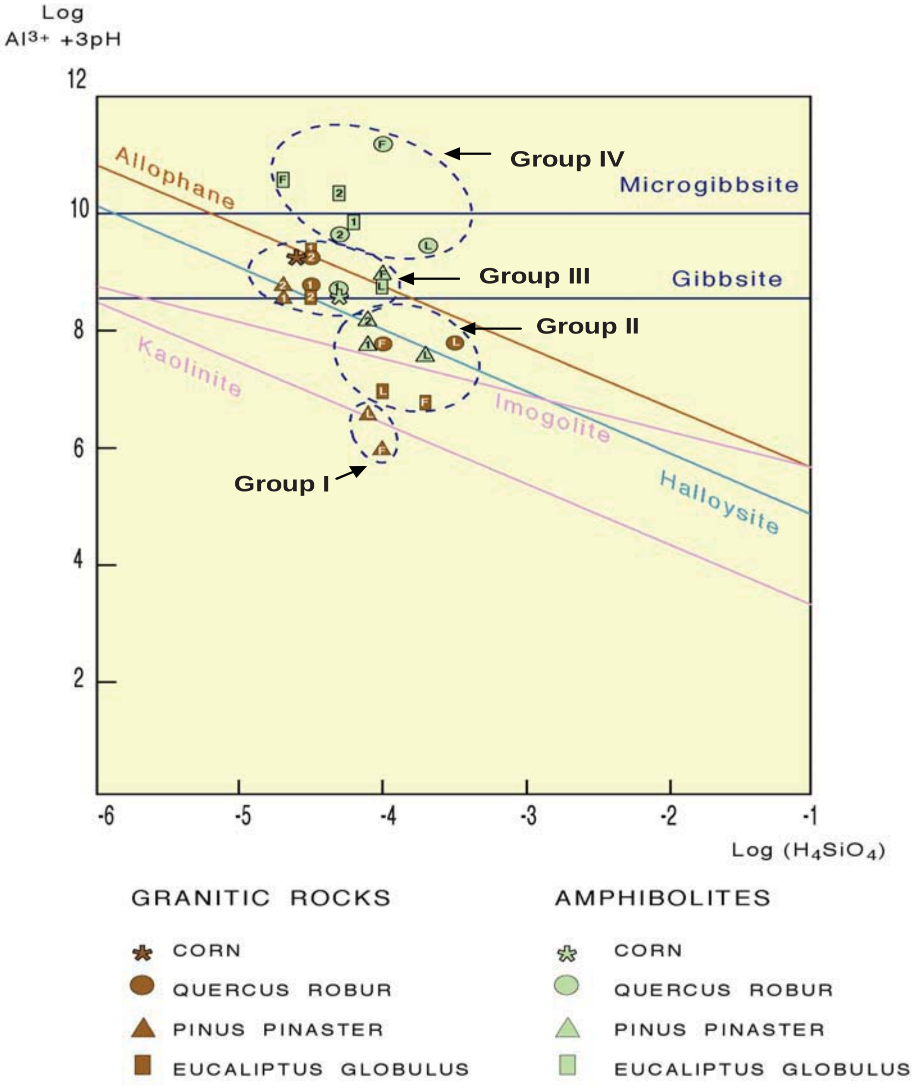


Figure 1. Soil solution equilibrium data for the SiO_2-Al_2O_3-H_2O system. Group I: None of the minerals is stable. Concentration of Al controlled by organo-Al complexes. Strong acid-complexolysis. Group II: Kaolinite stable, gibbsite unstable. Concentration of Al controlled by organo-Al complexes and kaolinite. Moderate acid-complexolysis. Group III: Kaolinite stable, gibbsite saturation. Concentration of Al by gibbsite of different degrees of crystallinites. Acidolysis. Group IV: Kaolinite stable, gibbsite and allophane saturation. Concentration of Al controlled by microcrystalline gibbsite. Andic character. Moderate acidolysis.

The L and F layers of the other two GR soils (under eucalypt and under oak stands), together with the L layer of the AMP-P soil, were all included in the second group of samples – group II - (Figure 1), which also corresponds to a very acidic system with an important presence of free organic acids (as estimated from the pH-NaF values; Table 2), but with some mineral saturation and with kaolinite as the most thermodynamically stable mineral, occurring along with metastable forms of short-range ordered 1:1 aluminosilicates, such as imogolite and halloysite, in some samples. The saturation index of Al ranged between 6.5 and 7.7 (Figure 1; Table 3), and was thus below the saturation index of gibbsite. Taking into account that kaolinite crystallizes very slowly, mineral neoformation should be practically negligible under the present conditions and, therefore, Al mainly forms bonds with organic acids.

Finally, the L and F layers of the other AMP soils (under eucalypt and under oak) were included in the third and forth groups of soils. In group III, the Al saturation index ranges between 8.2 and 9.0, indicating that the system is evolving towards the formation of kaolinite, although metastable forms, such as gibbsite, halloysite, and imogolite (Figure 1), and boehmite and alunite (not shown) may also exist. In group IV, the saturation index is so high (> 9.0) that the solutions are even oversaturated with allophanic compounds (Figure 1).

Independently of the groups identified, none of the Al_p/C_p nor $(Al_p + Fe_p)/C_p$ ratios in any of the organic layers studied were >0.1 (Table 2). On the basis of the amount of functional groups of humic substances, the maximum capacity of the OM to complex metals is indicated by a metal/C molar ratio (in the pyrophosphate extract) of between 0.1 and 0.2 (Higashi et al., 1981; Higashi, 1983; Dahlgren et al., 1993), although the critical ratio is dependent on pH (Buurman, 1985). The results therefore indicate that, independently of whether there was a stable mineral phase or not, in all cases, the OM of the litter samples was undersaturated with metals.

The higher acidity of the GR systems, in relation to the AMP systems, is mainly attributed to (i) the elemental composition of the parent materials (the former is poorer in bases and, thus, more acidic), (ii) the weatherability of the materials, as the GR rock is less weatherable than the AMP material, and (iii) the fact that soils developed from GR rock studied here are excessively well drained, implying that the percolating water has little time to interact with the mineral phase and therefore to allow the formation of secondary aluminosilicates (Macías & Chesworth, 1992). The effect the elemental composition of the parent material on that of litter and Ah horizons is clearly shown in the concentrations of CaO of these reservoirs (Figure 2). Concentrations of CaO in the litter were significantly lower ($P<0.05$) in the GR soils than in the AMP soils (L layers: 5.6 compared with 14.5 g kg^{-1}, and F layers: 0.8 compared with 7.6 g kg^{-1}, respectively) (Figure 2A-B). Moreover, CaO contents were always greater in the L than in the F layers and Ah horizons (Figure 2). This was attributed to the effect of the biotic pump produced by forest stands; the concentration effect of base cations in the L layers can also be observed in the Chesworth diagram (Figure 3) (Chesworth, 1973), with percentages of CaO and MgO in the L layer being even greater than those of the fresh (AMP-FR, GR-FR) and weathering materials (AMP-WR, AMP-WR) (Figure 3). This was not only due to an increase in the absolute concentration of bases (Figure 2), but also to the low mobility of Fe, Si, and Al in relation to that of Ca, Mg and K. In contrast, the concentration effect of base cations in the F layers was almost negligible (Figure 2 and 3), with values falling close to those of the Ah horizons (Figure 3), and all very close to the area typical of the "residual system" described by Chesworth (1973). This effect was independent of lithology, although the effect of concentration of Ca in the litter relative to that in the Ah horizons was more evident in the L layers of the GR soils than in the AMP soils (Figure 2), despite the higher concentrations of Ca in the latter (Figure 2; Figure 3).

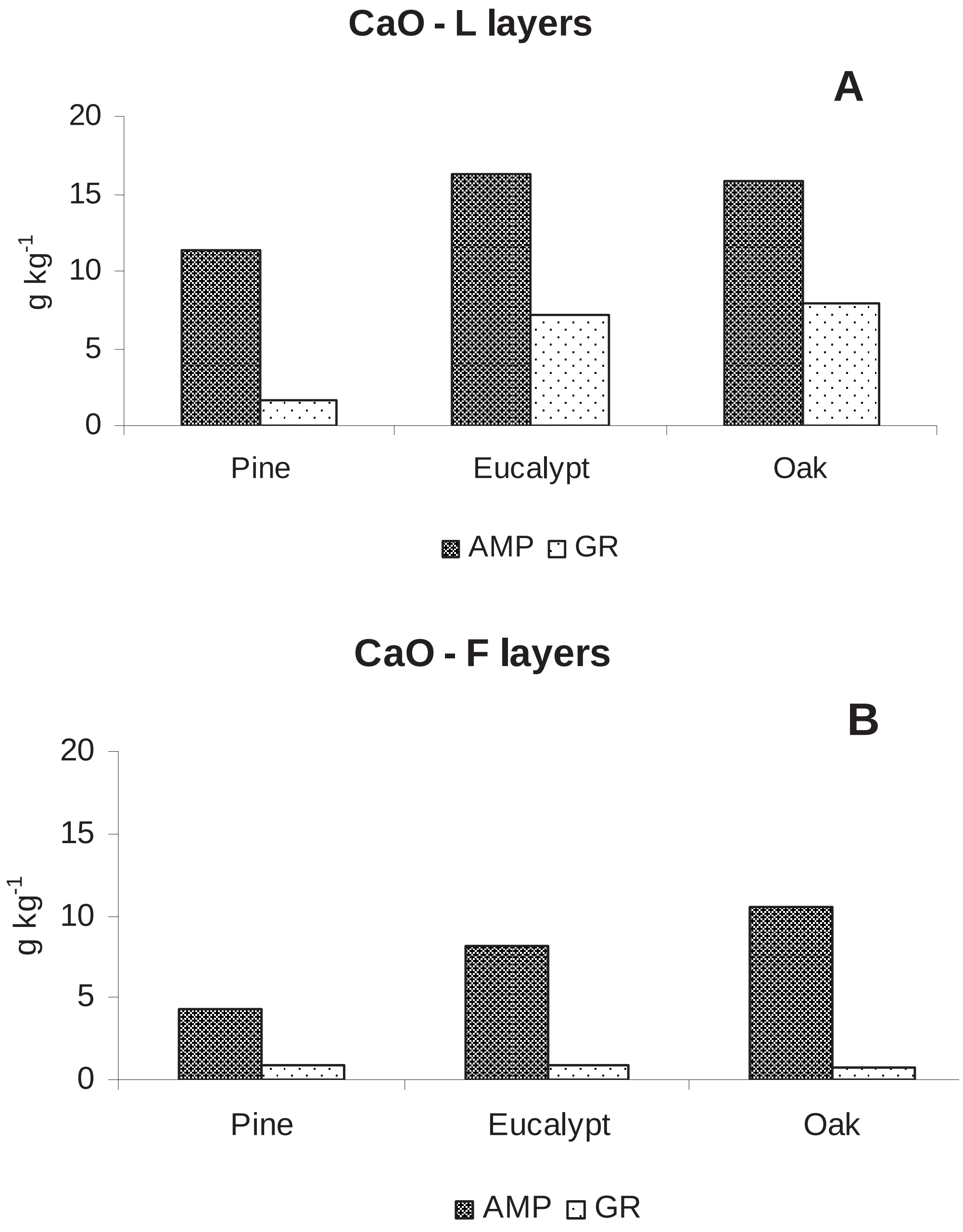


Figure 2. (Continued)

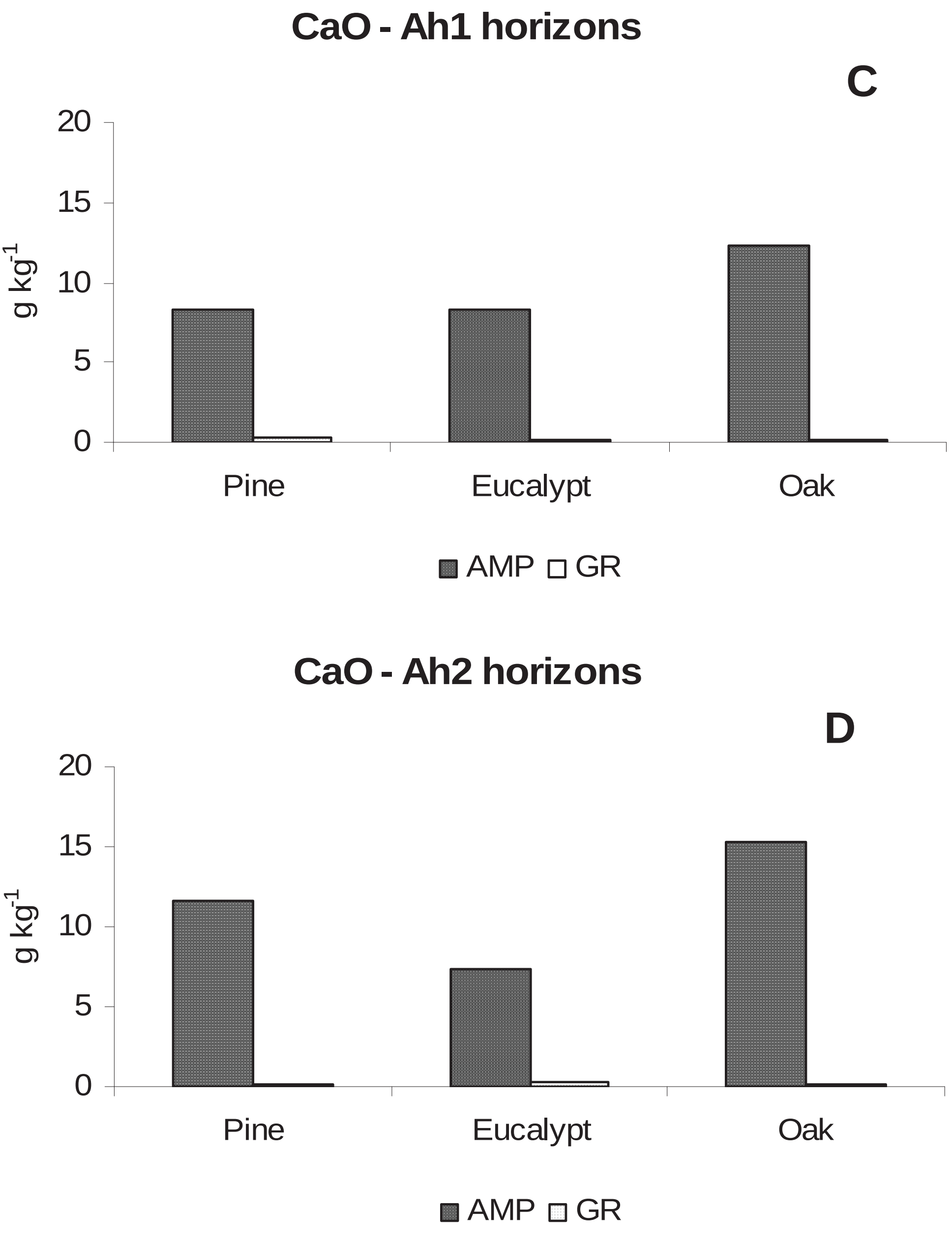


Figure 2. Mean concentrations of CaO in the L (a) and F (b) layers and Ah1 (c) and Ah2 (d) horizons, grouped by the different forest stands studied.

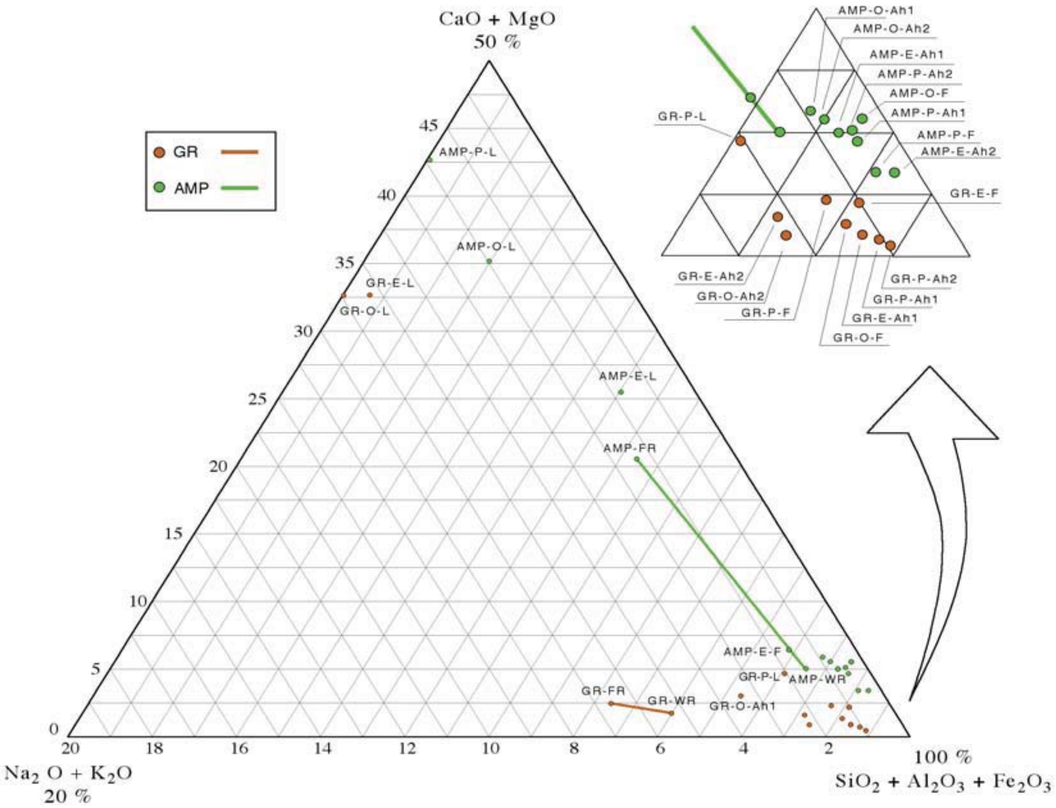


Figure 3. Chesworth diagram of the samples studied.

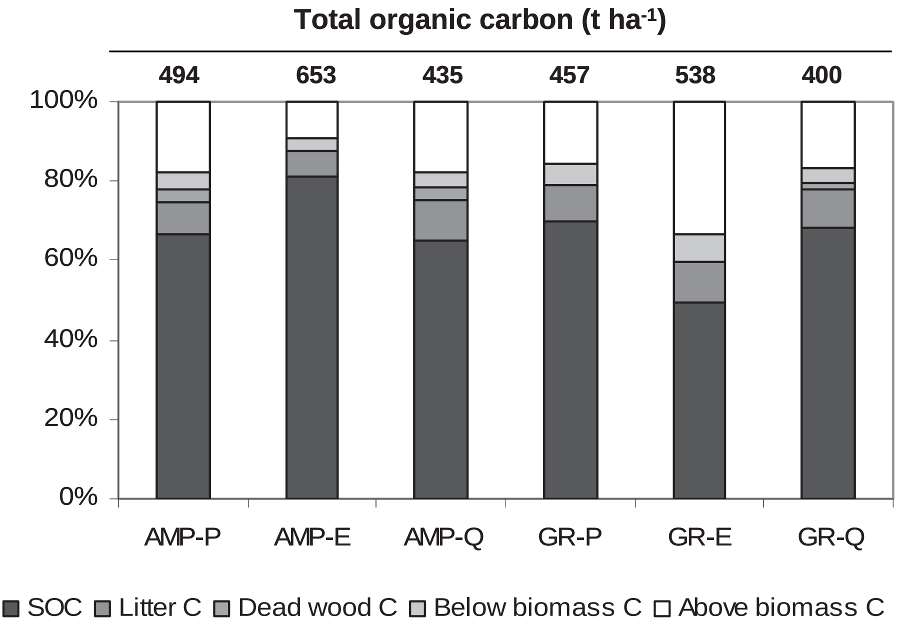
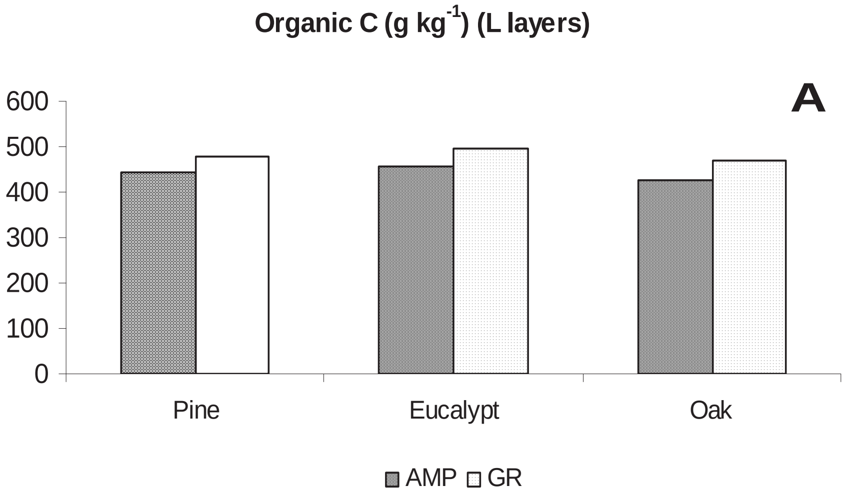
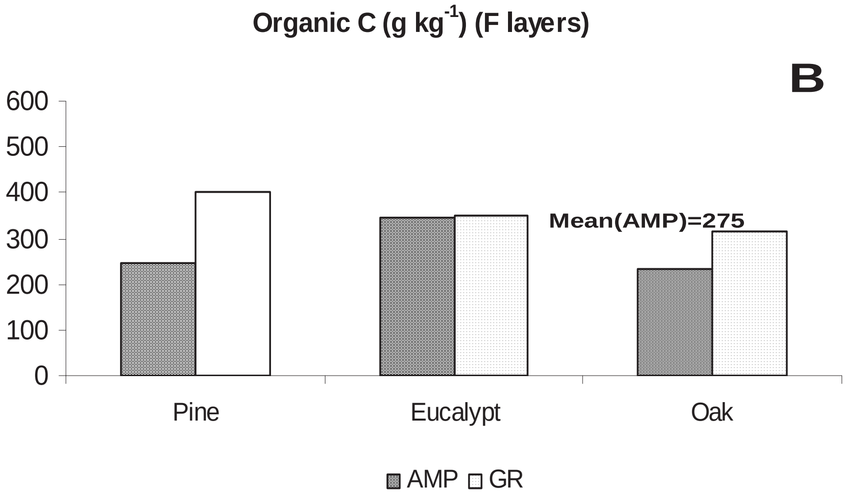


Figure 4. Percentage distribution of total organic C in the different pools identified within each forest ecosystem.

In summary, conditions in the GR litter systems, especially under pine and eucalypt, are dystrophic, whereas in the AMP litter systems they are more eutrophic. Acid-complexolysis dominates in the former systems, with the presence of strongly complexing organic acids (Camps Arbestain et al., 2003), which lead to the destruction of all minerals, except quartz. Under these conditions, organic acidity and complexing ability dominate in the systems, in contrast with the AMP litter systems, especially in the F layers under eucalypt and oak, which are governed by CO_2-acidity. All this may affect the characteristics of OM and the microbial activity in these soils, as will be discussed in the following section.

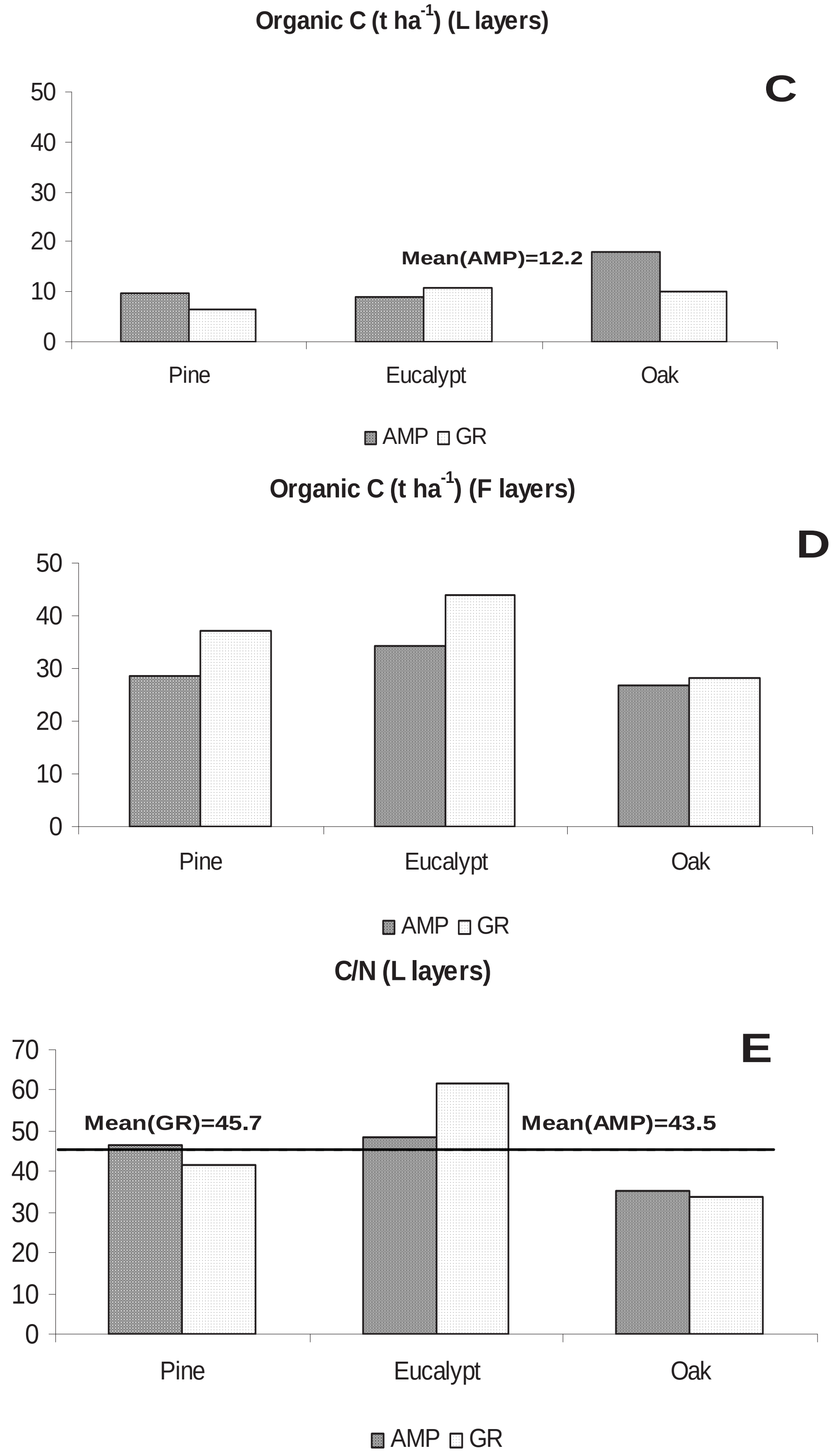


Organic C (g kg^{-1}) (L layers)



Organic C (g kg^{-1}) (F layers)

Figure 5. Continued on next page.



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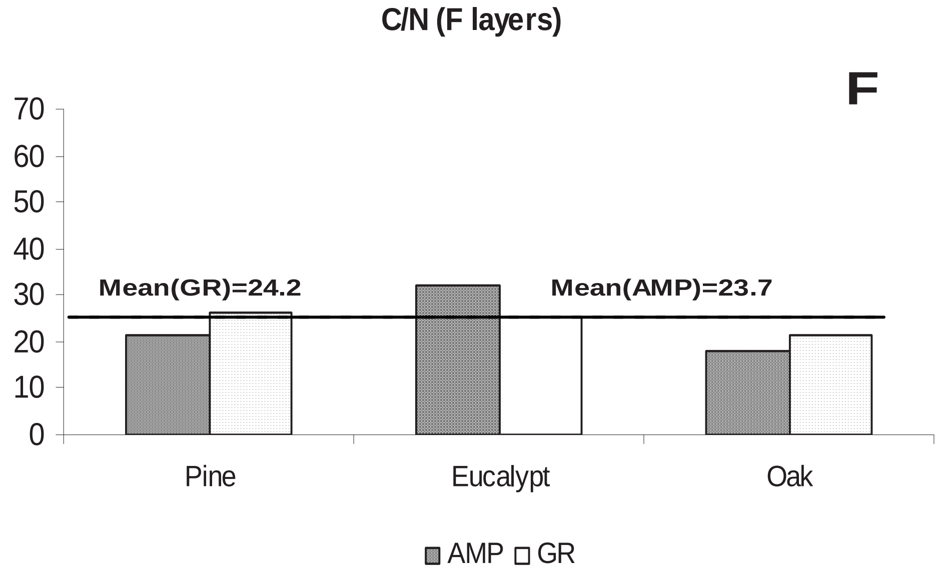


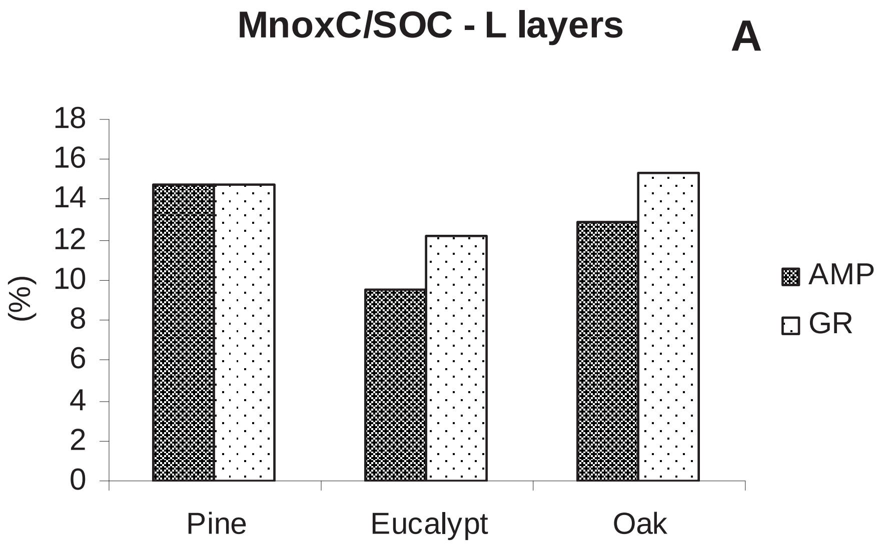
Figure 5. Organic C concentrations (a and b) and contents (c and d), and C/N ratios (e and f) of the L and F layers, grouped by the different forest stands studied.

Characterization of the Organic C Pools in Litter

In the present study, the presence of organic C in the litter (L and F layers) accounted for 7-10% of total organic C of the ecosystem, down to the lowest limit of the Ah horizons (Figure 4), as calculated from estimations of organic C stocks for each of the reservoirs per unit of surface (t ha^{-1}). The concentration of total organic C in the L and F layers was always higher (significantly different at $P<0.01$ and 0.10, respectively) in the GR than in the AMP soils (Figure 5A-B), with mean values of 481 and 354 g C kg^{-1} for the L and F layers of the GR soils, respectively, and 441 and 275 for the L and F layers of the AMP soils, respectively. When the total amounts of organic C of these horizons were considered rather than concentrations, the same trend was observed in the F layers (Figure 5D) (means: 36.5 and 29.9 t C ha^{-1}, for the GR and AMP soils, respectively), but not in the L layers (Figure 5C) (means: 9.1 and 12.2 t C ha^{-1}, for the GR and AMP soils, respectively), mainly because the amount of organic debris present at the surface differed widely among soil profiles (Table 2; L layers depths).

As far as litter composition is concerned, there were no significant differences (at $P<0.10$) between the ADF values (assumed to estimate cellulose + lignin) of the two groups of soils, with means of 64 and 61%, for the GR and AMP soils, respectively (Table 4). In contrast, the NDF values, which were assumed to estimate cellulose + hemicellulose + lignin, and the ADL values, which were assumed to estimate lignin, were consistently higher in the GR soils than in the AMP soils (means NDF: 69 and 61%; means ADL: 40 and 37% for the GR and AMP soils, respectively), especially in the oak and pine stands. Moreover, the NDF-ADF values, which were assumed to estimate hemicellulose, were significantly higher ($P<0.05$) in the GR than in the AMP soils (means: 4.5 and 0.4%, respectively). The results obtained thus suggest that decomposition of litter is probably faster in the AMP soils than in the GR soils, because of the existence of less dystrophic and less acidic conditions of the former, thereby leading to a lower concentration organic C and lower presence of fresh plant tissue components in the decomposing organic debris. Acceleration of litter decomposition was observed when the Ca concentration and pH of acidic forest soils was increased by the addition of lime, thereby decreasing Al toxicity (Bauhus et al., 2004). The latter authors noted that, with this practice, a moder humus of an acid forest soil turned into a mull-moder type humus.

The mean percentages of MnoxC/SOC in the L and F layers were significantly higher ($P<0.10$) in the GR soils than in the AMP soils (L layers: 14.1 compared with 12.4%; F layers: 16.5 compared with 14.7%, respectively) (Figure 6A-B), which may indicate the presence of a less decomposed OM - and therefore more oxidizable OM - in the litter of the GR soils than in that of the AMP soils, in agreement with the results discussed above. This method has been shown to be particularly sensitive to the presence of lignin and lignin-like compounds (Loginow et al., 1987; Tirol-Padre & Ladha, 2004; Skjemstad et al., 2006), which are also more abundant in the GR litter. Moreover, the mean percentages of MnoxC/SOC in the L layers (Figure 6A) were significantly lower ($P<0.05$) than in the F layers (Figure 6B) (means: 13.2 compared with 15.6%, respectively). These results were somewhat unexpected, as litter is assumed to be less decomposed in the L layers than in the F layers, and thus, the former should be more susceptible to being oxidized. However, the results obtained may be explained by the fact that part of the oxidable C present in the L layers may be still protected by the plant architecture (e.g., cellulose within lignin). In any case, it should be remembered that the rate and extent of OM oxidation with $KMnO_4$ is governed by characteristics such as functional groups, stereochemistry and solubility, with anionic forms generally being more readily oxidized than neutral and cationic forms (Clapp et al., 2005). More research is needed in this area to discern the reasons behind the patterns observed in these samples.



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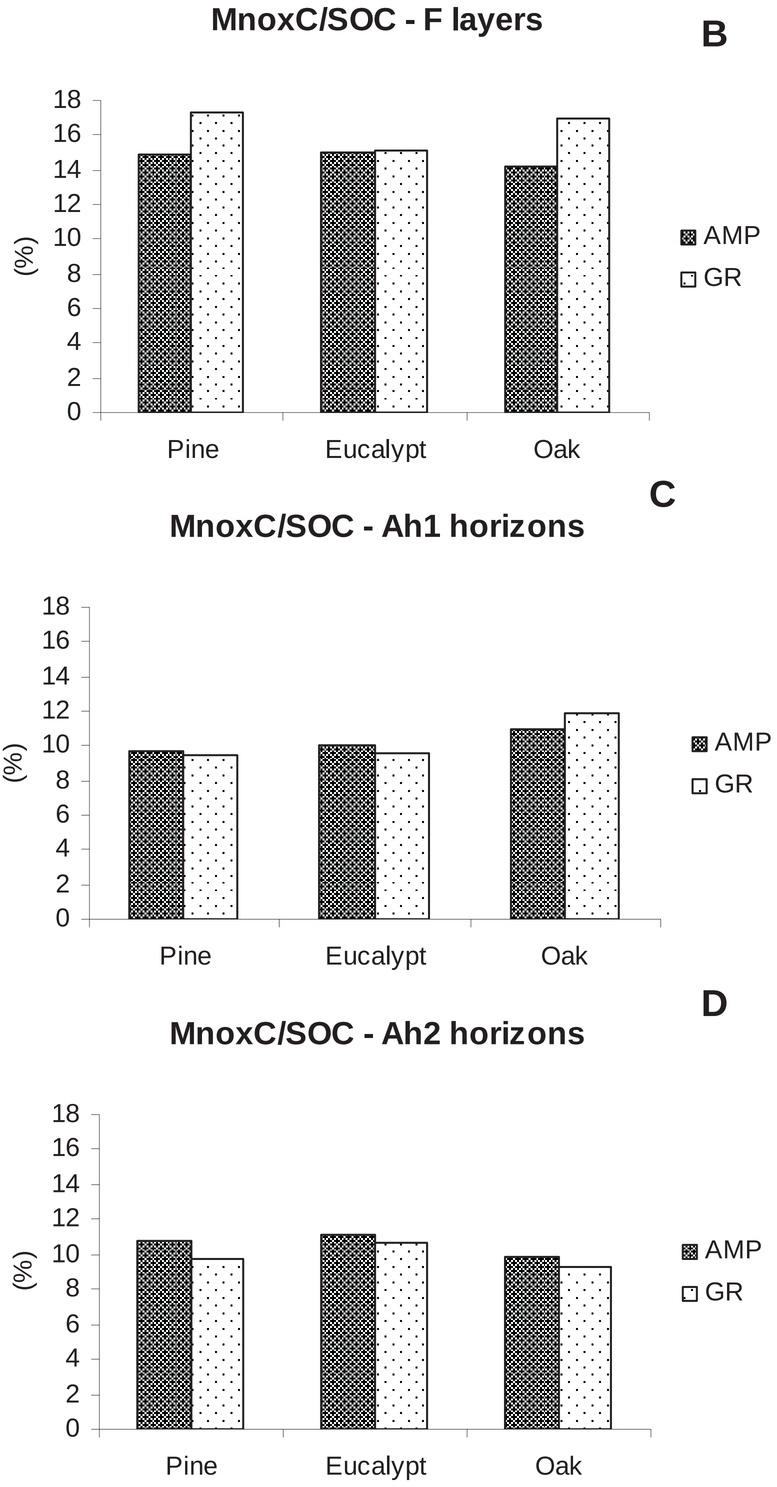
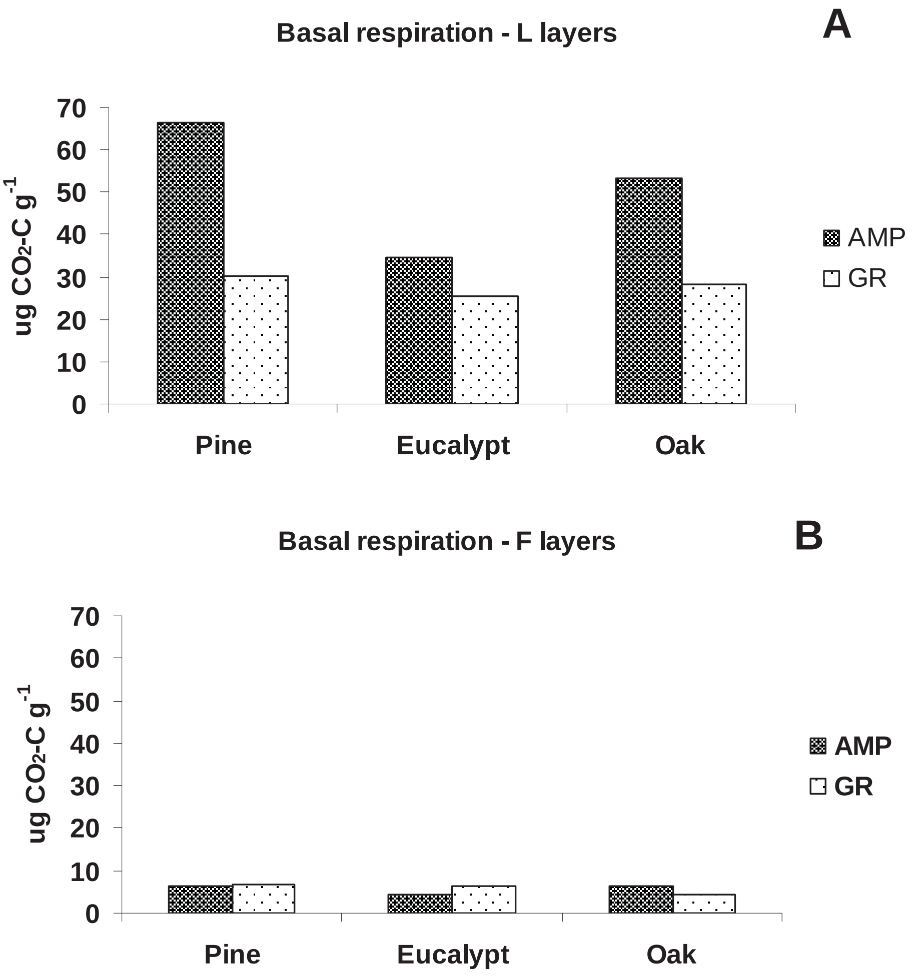


Figure 6. Percentages of MnoxC/SOC in the L (a) and F (b) layers and Ah1 (c) and Ah2 (d) horizons, grouped by the different forest stands under study.

The hot-water extractable C (HWC) of the L layers was also determined. Ghani et al. (2003) proposed this extraction as a means of estimating the fraction of the labile soil OM that is closely related to C_{mic}, as well as to soluble soil carbohydrates and mineralizable N. However, in the present study, C_{mic} was not significantly correlated with HWC at $P<0.05$ (Table 4), although a positive correlation was observed ($r = 0.69$); the sample with the highest C_{mic}, AMP-O (10.1 g C_{mic} kg^{-1}) was also that with the highest HWC (26.0 g HWC kg^{-1}). Litter under pine stand had the lowest HWC in both sites (GR and AMP), thus indicating a forest species effect, whereas no clear relationship was found between HWC and type of parent material (Table 4), as expected. Values of C_{mic} ranged between 3.4 and 10.1 mg C_{mic} g^{-1} soil in the L layers, and between 1.8 and 5.2 mg C_{mic} g^{-1} soil in the F layers (Table 3), which represents between 0.7 and 2.4% of the organic C in the L layers, and between 0.5 and 1.7% in the F layers (i.e., C_{mic}-to-C_{org} percentages). No clear effects of parent material were observed in either C_{mic} or C_{mic}-to-C_{org} (%) (Table 4).



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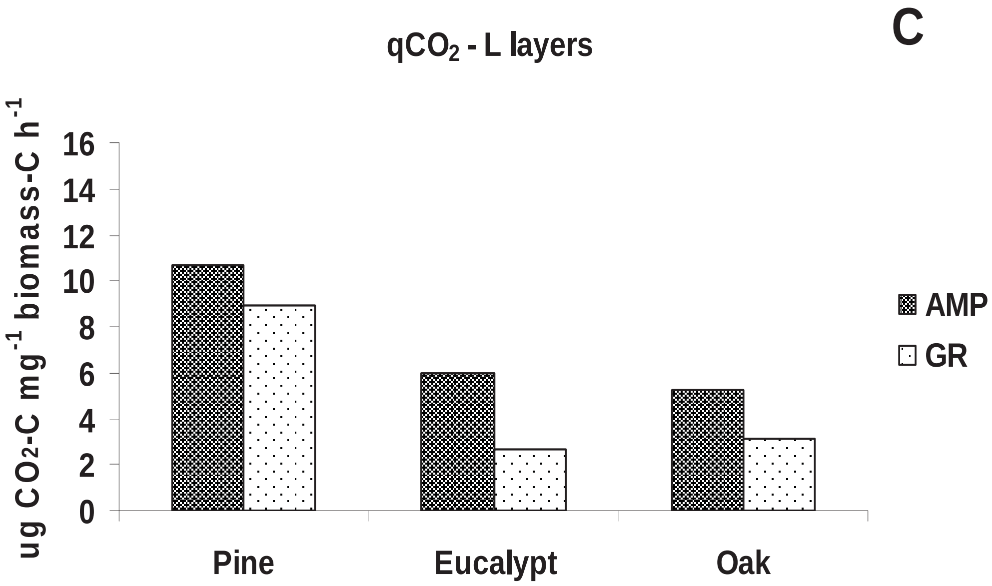

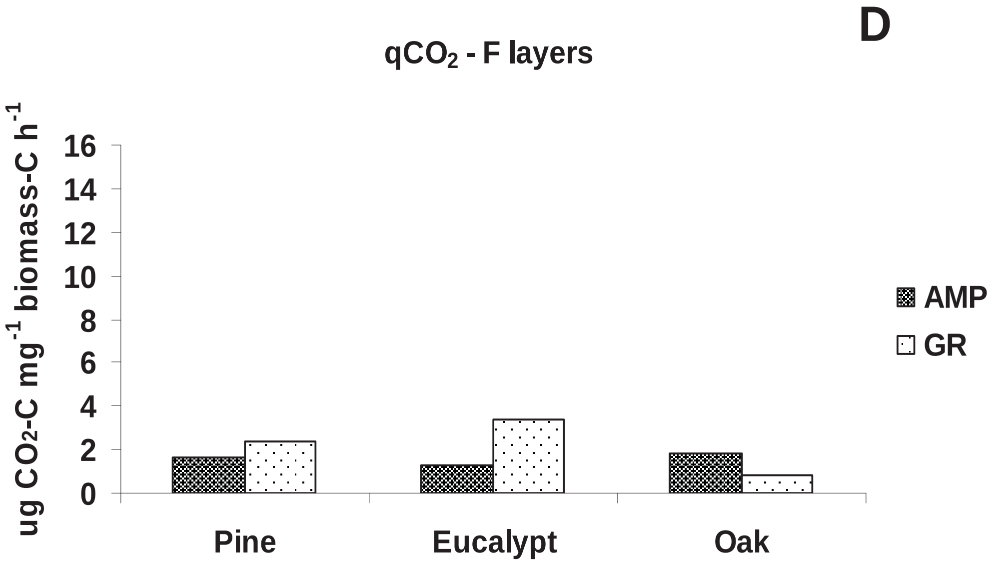

Figure 7. Basal respiration (a and b) and metabolic quotient (c and d) of the L and F layers, grouped by the different forest stands under study.

Basal respiration in the AMP L layers was significantly higher ($P<0.05$) than in the GR L layers (means: 51.5 compared with 28.0 µg CO_2-C g^{-1} h^{-1}, respectively) (Figure 7A), whereas no clear pattern was observed in the F layers (Figure 7B) (means: 5.6 and 5.8 µg CO_2-C g^{-1} h^{-1}, respectively. Moreover, plant species did not have a clear effect on basal respiration, which is consistent with the findings of Raich & Tufekcioglu (2000), i.e., that vegetation type had relatively little effect on soil respiration rates. When basal respiration was reported per unit of biomass, i.e. the specific respiration of the biomass, qCO_2 (μg CO_2-C mg^{-1} biomass-C h^{-1}) (Figure 7C-D), mean values of the AMP L layers were again significantly higher ($P<0.05$) than those of the GR L layers (means: 7.3 compared with 4.9 μg CO_2-C mg^{-1} biomass-C h^{-1}, respectively) (Figure 7C), and no clear pattern was observed in the F layers (means: 1.6 compared with 2.2 μg CO_2-C mg^{-1} biomass-C h^{-1}, respectively) (Figure 7D). Blagodotskaya & Anderson (1998) observed a higher qCO_2 in soils of low pH than in neutral soil, in contrast to the present results. However, the pH range in the present study was probably not wide enough to allow detection of the same patterns as observed by these authors. In the present study, species had an effect on qCO_2 in both organic horizons as, in the L layers, the mean qCO_2 of pine soils (9.8 μg CO_2-C mg^{-1} biomass-C h^{-1}) was more than twice that in eucalypts and oak soils (4.3 and 4.2 μg CO_2-C mg^{-1} biomass-C h^{-1}, respectively) (Figure 7C). Moreover, in the F layers, this pattern was also observed for the GR samples (Figure 7D). Therefore, oak, which was the native forest stand in the area, generally had the lowest qCO_2 values (Figure 7C-D) and the lowest C/N ratio of the litter samples studied (Figure 5E-F). Blagodotskaya & Anderson (1998) compared acid soils under conifer stands (spruce) and deciduous stands (beech) and observed a higher qCO_2 in the former, as in the present results. Moreover, Wardle (1993) and Wardle et al. (1995) indicated that despite the general trend of decreasing qCO_2 throughout litter decomposition, a significant increase could eventually occur in types litter resistant to decomposition, which could be the case with pine. Wardle & Ghani (1995) suggested that factors able to increase values of qCO_2 during ecosystem development are (i) stress (e.g., pH), and (ii) disturbance, either of which could explain the higher qCO_2 in pine and eucalypt plantations than in oak forest.

Thus, in summary, the effect of parent material on the characteristics of the organic matter of the litter samples was mainly observed in the concentration of total organic C, oxidability, basal respiration, and the metabolic quotient (qCO_2), Overall, it appears that the higher acidity and dystrophia observed in the GR litter than in the AMP litter slowed down the microbial decomposition of the organic debris, explaining the higher concentration of total organic C and oxidability by $KMnO_4$ of the litter present in the GR materials than in the AMP soils, as well as the lower basal respiration and metabolic quotient of the former. On the other hand, the effect of the forest species on the characteristics of the OM of the litter samples was mainly observed in the C/N ratio and in the qCO_2, and the behaviour of the oak litter generally differed from that of the other two species. The more aggressive forest management of the pine and eucalypt stands (greater disturbance), together with the greater recalcitrance and acidity of the pine litter (greater stress), may explain the differences observed in the qCO_2 among the three forest species studied, although more research is needed to confirm this.

Table 4. Estimated composition of litter using different extractants. AMP = amphibolite and GR =granite

		Acid detergent fibre		Neutral detergent fibre		Acid detergent lignin		DOC[†]		Water-soluble C		Hot water-soluble C		Microbial biomass C		C_{mic}-to-C_{org}	
Litter layers	Forest species	AMP	GR	AMP	GR	AMP	GR	AMP	GR	AMP	GR	AMP	GR	AMP	GR	AMP	GR
		%DM		%DM		%DM		µg C g^{-1} litter		µg C g^{-1} litter		µg C g^{-1} litter		µg biomass C g^{-1} litter		%	
L	Pine	62	70	62	76	36	43	1752	1912	6409	14965	10990	16119	6252	3397	1.41	0.71
	Eucalyptus	63	62	63	64	38	38	1158	2680	11306	25251	17300	23007	5830	9622	1.28	1.94
	Oak	58	61	59	66	37	39	1822	1670	32543	17127	26010	17337	10109	9014	2.38	1.92
	Mean‡	61a	64a	61a	69a	37a	40a	1577a	2087a	16752a	19113a	19100a	18821a	7397a	7344a	1.69a	1.52a
F	Pine	-	-	-	-	-	-	934	693	-	-	-	-	3844	2842	1.57	0.71
	Eucalyptus	-	-	-	-	-	-	700	568	-	-	-	-	3236	1847	0.94	0.53
	Oak	-	-	-	-	-	-	706	888	-	-	-	-	3496	5227	1.50	1.67
	Mean‡							780a	716a					3305a	3525a	1.33a	0.97a

[†] Dissolved organic C determined in a 1:10 litter:water mixture equilibrated for three days .

[‡] Mean values of each variable studied within AMP and GR rows followed by the same letter are not significantly different at the 0.05 level of probability.

Table 5. Values of several physicochemical properties of the different Ah samples

Hor.	Sample code	Depth	pH-H_2O	pH-ClK	pH-NaF	Al_p	Fe_p	C_p	Al_p/C_p	$(Al_p+Fe_p)/C_p$	Coarse sand	Fine sand	Silt	Clay	Texture [†]	Moisture content[‡]	Bulk density
		(cm)				(g kg^{-1})			(mol mol^{-1})		(%)					(%)	g cm^{-3}
Ah1	AMP-P	0-25	4.92	4.12	11.50	27.66	11.90	83.3	0.15	0.18	4.3	19.2	66.7	9.8	si-l	37.8	0.75
	AMP-E	0-25	4.94	4.13	11.42	29.34	10.74	102.1	0.13	0.15	5.3	21.4	46.7	26.6	l	45.0	0.71
	AMP-O	0-25	4.95	4.28	11.26	21.07	10.78	66.9	0.14	0.18	6.7	22.6	58.3	12.4	si-l	30.7	0.82
	GR-P	0-25	4.69	3.89	10.90	10.03	11.88	48.5	0.09	0.14	22.3	36.3	30.5	10.9	sa-l	26.5	0.97
	GR-E	0-25	4.32	3.66	9.30	10.07	5.98	27.8	0.16	0.21	17.1	44.9	32.4	5.6	sa-l	17.2	1.00
	GR-O	0-25	4.21	4.00	10.81	19.34	15.38	59.7	0.14	0.20	11.5	37.2	41.2	10.1	sa	13.2	0.98
	AMP[¶]		4.94a	4.18a	11.39a	26.02a	11.14a	84.1a	0.14a	0.17a	5.5a	21.1a	57.2a	16.3a		37.8a	0.76a
	GR[¶]		4.41b	3.85b	10.34b	13.14a	11.08a	45.3a	0.13a	0.18a	17.0b	39.5b	34.7b	8.5a		19.0a	0.98b
Ah2	AMP-P	25-40	4.76	4.24	11.53	22.83	10.63	58.1	0.18	0.21	3.7	17.1	68.7	10.4	si-l	38.6	0.83
	AMP-E	25-50	5.07	4.13	11.45	28.18	10.19	82.9	0.15	0.18	2.2	14.8	53.7	29.4	si-c-l	45.2	0.75
	AMP-O	25-40	5.33	4.33	11.29	21.60	13.25	44.5	0.22	0.28	11.2	23.9	52.3	12.6	si-l	31.3	0.73
	GR-P	25-40	4.79	4.14	11.35	16.29	14.81	48.4	0.15	0.22	34.9	29.2	29.1	6.9	sa-l	32.5	1.01
	GR-E	25-50	4.75	4.10	11.18	15.61	8.74	38.5	0.18	0.23	11.7	42.9	37.8	7.7	sa-l	24.8	1.04
	GR-O	25-50	4.68	4.01	10.55	20.99	15.55	35.5	0.28	0.38	12.9	38.4	39.4	9.5	l	21.2	0.98
	AMP[¶]		5.05a	4.23a	11.42a	24.20a	11.36a	61.8a	0.18a	0.22a	5.7a	18.6a	58.3a	17.4a		38.4a	0.77a
	GR[¶]		4.74a	4.08a	11.03a	17.63a	13.03a	40.2a	0.20a	0.27a	19.8a	36.8b	35.4b	8.0a		26.1a	1.01b
Ap	AMP-C	0-25	5.18	4.30	10.70	5.4	10.59	35.7	0.17	0.24	2.8	16.1	34.5	46.6	c	7.4	1.10
	GR-C	0-25	4.81	4.39	10.92	5.0	7.79	18.5	0.28	0.37	11.9	46.3	34.4	7.5	sa-l	18.5	0.97

[†] Si-l = silty-loam; l = loam; sa-l = sandy-loam; sa = sandy; si-c-l = silty-clay-loam; clayey = c.

[‡] Moisture content of soils at the time of sampling, determined after drying at 105ºC.

[¶] Mean values of each variable studied within AMP and GR rows followed by the same letter are not significantly different at the 0.05 level of probability.

Soil Organic Matter

Chemical Characterization of Soil Organic Matter Present in the Ah Horizons

The pH values of the umbric Ah1 horizons in the GR soils were significantly lower (at $P<0.05$) than those of the fulvic A1 horizons in the AMP soils (means: 4.4 compared with 4.9, respectively), whereas no significantly differences were observed in the Ah2 horizons, although the same trends were detected (means: 4.7 compared with 5.1, respectively) (Table 5). As indicated above, at pH values < 4.2-4.4, as in the organic horizons of the GR soils, the acidity of the system is determined by free organic acids. However, the pH increases with depth, while the activity of organic acids decreases because they become buffered by the mineral alkalinity of the soil, and the acid-base equilibrium is determined by CO_2 and hydroxyaluminum ions (Macías & Calvo de Anta, 1992). The observed increase in pH was paralleled by a decrease in the EC of the equilibrium solutions, in which the concentration of all major anions and cations decreased sharply with depth, with the lowest decreases in Al (Table 3). The Al_p/C_p and $(Al_p+Fe_p)/C_p$ molar ratios of the Ah1 horizons ranged between 0.09 to 0.21 (Table 5), with mean values of 0.14 and 0.18, respectively, indicating saturation of SOM with Al and Fe. Thus, the acidity of the SOM decreased, as the interaction of the soil solution with the mineral phase became more intense, and metal-saturation of SOM increased. The Al_p/C_p and $(Al_p+Fe_p)/C_p$ molar ratios in the Ah2 horizons ranged between 0.15 and 0.38 (mean values 0.19 and 0.25, respectively; Table 5). Values of the ratio of > 0.2 may indicate the presence of polymeric metal-OH forms, which can react with negatively charged organic compounds, and are susceptible to being dissolved by sodium pyrophosphate (Kaiser & Zech, 1996). There were no significant differences between the two types of parent materials ($P<0.05$), but a species effect was observed in the Ah2 horizons, with the values of ratios for the oak species always being the highest (Table 5).

In the mineral surface horizons, the reactivity to the NaF test was high in both groups of soils, with mean values of 10.3 and 11.0 for the Ah1 and Ah2 horizons of the GR soils, respectively, and of 11.4 and 11.4, for the same horizons from the AMP soils, respectively (Table 5). The high NaF-pH values indicate the presence of reactive Al in these horizons, which are more abundant in the AMP soils (Camps Arbestain et al., 2003). However, differences in mean NaF-pH values in these two groups of soils were not significantly different ($P<0.05$). As this measurement is a qualitative indicator of the presence of reactive Al it therefore cannot be used to distinguish differences in their total amounts, in contrast to other measurements, such as Al_p or Al extractable with ammonium oxalate. The Al_p data (Table 5) reflects the significantly greater ($P < 0.10$) presence of Al-humus complexes in the AMP than in the GR soils (26.0 vs 13.1 g kg^{-1}), and these compounds, together with short-range order compounds are susceptible to reacting with NaF. Reactive Al compounds, mostly short-range order compounds -as well as stable organo-Al complexes- have frequently been found in large quantities in incipient soils from Galicia derived from basic and metabasic materials (Macías et al., 1978; García-Rodeja et al, 1987).

Examination of the solution equilibria systems displayed in Figure 1, reveals that the Ah horizons developed from GR rock are included in group III, in which the Al saturation index ranges between 8.2 and 9.0, and which indicates that the system evolves towards the formation of kaolinite, although metastable forms, such as gibbsite, halloysite, and imogolite (Figure 1), and boehmite and alunite (not shown) may also occur. The Ah horizons of the eucalypt and oak stands developed from AMP materials are mostly included in group IV, in which the Al saturation (> 9.0) is so high that the solutions are even oversaturated with allophanic compounds (Figure 1), which contrast with those of pine stands developed from the same materials, which are included in group I. In the group IV systems, non crystalline metastable forms can interact with secondary organic components leading to the formation of abundant and probably stable, organo-mineral bondings, and giving rise to the typical aluandic character of these soils. Buurman (2006) suggested that the high water retention of allophanic Andosols (containing primary aggregates of around 10 μm) under perudic conditions, may cause the slow decomposition of secondary OM and, therefore, the well-known accumulation of SOM in these soils. To our knowledge, there are no studies of aluandic Andosols in NW Spain that attribute the high water retention of these soils, as an additional mechanism involved in the accumulation of SOM. In the present study, soil texture of the aluandic Andosols ranged from loam, to silty loam, and to silty clay loam, whereas it was sandy loam for all Umbrisols (Table 2). The coarser texture of the GR soils was mainly related to the higher presence of quartz in the granite rock compared with the AMP materials, and resulted in a lower water holding capacity of the former, but differences may have been further accentuated by the presence of amorphous compounds in the AMP soils. Differences in the water holding capacity between the two groups of soils were confirmed by the soil moisture contents at the time of sampling - which was carried out on the same dates for both types of soils - with those of the AMP samples generally being higher than those of the GR samples (Table 5), thus indicating faster drainage and higher susceptibility of the GR soils to drying under identical climatic conditions to those to which the AMP soils are subject. Nonetheless, more research is needed in the study region to determine the extent to which the different water moisture regimes of the AMP and GR soils affect the quantity, quality, and dynamics of SOM in these ecosystems, as proposed by Buurman (2006) for allophanic Andosols under perudic conditions.

Characterization of the Organic C Pools in the Soil Organic Matter Present in the Ah Horizons

The amount of organic C present in the surface mineral horizons (Ah1 and Ah2 horizons) accounted for 50-82% of total organic C of the ecosystem (down to the lowest depth of the Ah horizons) (Figure 4), with mean values of 71 and 63% for the AMP and GR soils, respectively (not significantly different at $P<0.05$). The values provide a clear idea of the importance of the SOM stocks in forest ecosystems relative to those accumulated in the aboveground biomass, which ranged between 9 and 34%. The mean values of the organic C stocks accumulated in the Ah horizons were 381 and 286 t ha^{-1} for the AMP and GR soils, respectively (i.e. 8.3 and 6.5 t ha^{-1} cm^{-1}, respectively), which are well above the default values (*Tier 1* level) outlined in the IPCC Good Practice Guidance (IPCC, 2003) for surface horizons of soils under humid temperate conditions (e.g., 80 t ha^{-1} for the first 30 cm of Andosols; i.e., 2.7 t ha^{-1} cm^{-1}). This emphasizes the need for different countries to define C stocks for the different pedoclimatic regions and land-use systems, as required at the *Tier 2* level in the same guidance.

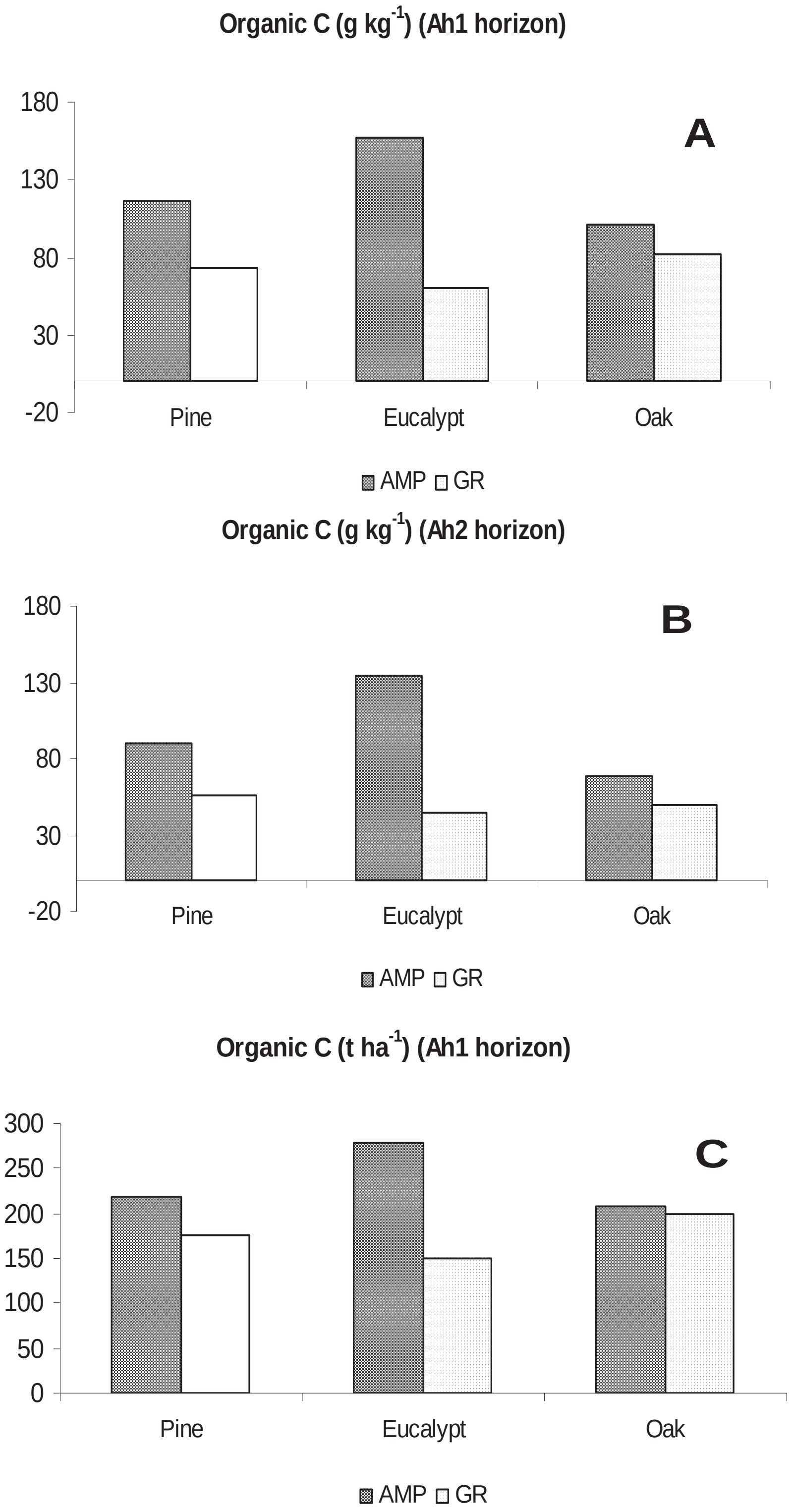

Figure 8. Continued on next page.

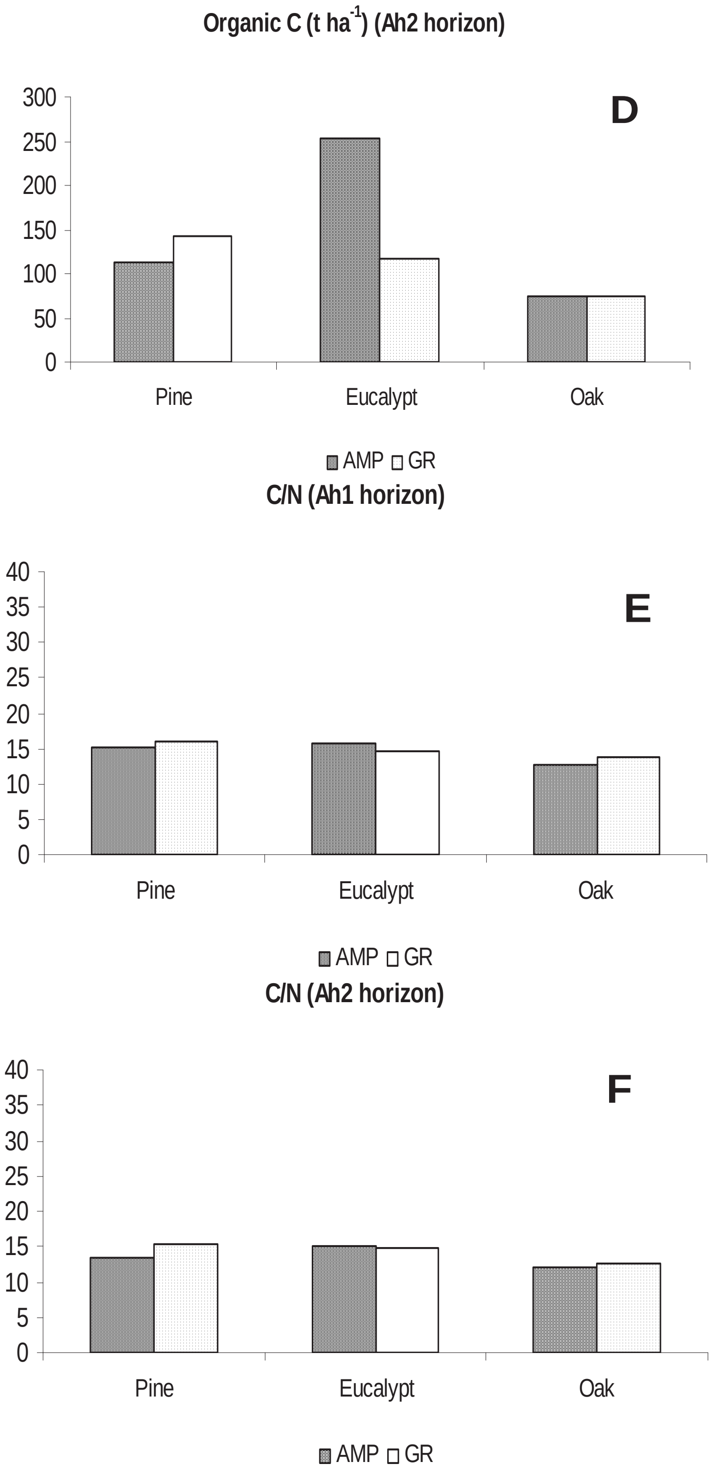

Figure 8. Concentrations (a and b) and contents (c and d) of organic C, and C/N ratios (e and f) of the Ah1 and Ah2 horizons, grouped by the different forest stands studied.

The concentration of total organic C in the Ah1 and Ah2 horizons was always higher (and significantly different at $P<0.10$) in the AMP than in the GR soils (Figure 8A-B), with mean values of 125 and 98 g C kg^{-1} for the Ah1 and Ah2 horizons of the AMP soils, respectively, and 71 and 51 g C kg^{-1} for the Ah1 and Ah2 horizons of the GR soils, respectively. Thus, the opposite pattern was observed in the mineral horizons (Figure 8A-B; AMP soils > GR soils) than in the organic horizons (Figure 3A-B; AMP soils < GR soils). When the total amounts of organic C of the Ah1 horizons were considered rather than concentrations, differences between the two groups of soils were reduced (Figure 8C) - because of the greater soil bulk densities of the GR soils than of the AMP soils (Table 5) (mean values 220 and 186 t ha^{-1}, respectively). Stocks of organic C in the Ah2 horizons did not follow a common trend (Figure 8D) as depths of these horizons varied among soil profiles (Table 5). Moreover, the concentration of total organic C in the surface horizons of two cultivated soils close to the AMP and GR forests were well below the values for the forest sites (43 and 48 g C kg^{-1} soil, respectively). The results suggest that the rapidly metabolized primary OM of the AMP soils becomes stabilized by reactive Al compounds, which are abundant in these soils, and which slow down the decomposition of secondary OM. In contrast, in the GR soils, the acidic and dystrophic conditions appear to lead to the slow decomposition of primary OM in the litter layers, but not in the more eutrophic Ah horizons. In fact, basal respiration per unit of organic C of litter layers were greater in the AMP soils than in the GR soils, whereas the inverse pattern was observed in the Ah layers (data not shown). All this may explain the existence of a moder type OM, in contrast to the Al-mull OM of the AMP soils.

The mean percentages of MnoxC/SOC in the Ah1 horizons did not differ significantly ($P<0.05$) in AMP and GR soils (means: 10.2 and 10.3%, respectively) (Figure 6C), but those of Ah2 did differ significantly between the two types of soils at $P<0.05$, with the mean of the AMP soils being greater than that of the GR soils (means: 10.6 and 9.9%, respectively) (Figure 6D). Thus, again, the pattern observed at depth was the opposite of that observed in the organic horizons (Figure 6A-B; AMP soils < GR soils). When comparing organic and mineral horizons, the results indicate that the content of permanganate-oxidizable C was always greater in the litter layers than in the Ah horizons (14.4 compared with 10.3%, respectively; Figure 6), as expected from the presence of less decomposed materials in the former. The mean percentages of MnoxC/SOC in the Ap horizons of the cultivated soils were 7.9 and 8.9%, for the AMP and GR soils, respectively, i.e. lower than in the Ah1 horizons of the forest soils, indicating that, in addition to a decrease in total organic C, cultivation probably accelerates decomposition of the most oxidable soil OC, leaving behind the least oxidable soil OC, in agreement with the previous results (Blair et al., 1995; Bell et al., 1998). The results of calculations made using the values corresponding to oak stands as reference values for natural soils and carried out on the basis of equal depth (down to 25 cm depth) indicate that the losses of organic C from the cultivated Ap horizons were 89 and 84 t ha^{-1} for the AMP and GR soils (43 and 42% lost, respectively), and 134 and 122 t ha^{-1}, respectively, when the litter layers were included (53 and 51% lost, respectively) in addition to soil organic C. When the same calculations were made on the basis of equal soil mass (35 cm depth for the AMP-O soil; 25 cm depth for the GR-O, AMP-C, and GR-C soils), the losses of organic C from the cultivated Ap horizons (down to 25 cm depth) were 138 and 84 t ha^{-1} for the AMP and GR soils, respectively (53 and 42%, respectively), and 182 and 122 t ha^{-1}, respectively, when the litter layers were included (60 and 51% lost, respectively). On the other hand, losses of MnoxC in the cultivated Ap horizons on the basis of equal depth (down to 25 cm depth) were 13 t ha^{-1} for both type of soils, and 20 t ha^{-1} when the litter layers were included in addition to soil organic C. When the same calculations were made on the basis of equal soil mass, the losses of organic C from the cultivated Ap horizons were 18 and 13 t ha^{-1} for the AMP and GR soils, respectively, and 24 and 20 t ha^{-1}, respectively, when the litter layers were included.

The similar ease of oxidation by $KMnO_4$ of the Ah1 horizons of both types of soils suggest that, despite the well-known ability of soils with andic properties to accumulate OM under natural conditions, the extent to which this becomes depleted after changes in land use, such as the conversion of forest soils to agricultural soils, may be similar in both types of soils. This is further corroborated by the observed decrease in the MnoxC/SOC ratio of the cultivated AMP and GR soils, and the estimated losses of total organic C with the change in land use, as estimated above. Verde et al. (2005) studied the effect of cultivation of soils with andic properties and observed high lability of the least stable organo-Al complexes, which were estimated by $CuCl_2$ extraction, with values in the agricultural soils being less than 40% of the corresponding values in the forest soils.

Overall, the results indicate that, in the GR soils, the type of pedogenesis taking place in the surface horizons is mainly determined by the lithology, with intense acidification (acid-complexolysis) associated with scarce or nil neoformation of secondary minerals in those compartments of greatest acidity (L and F) and abundance of aqueous and mobile organo-metal complexes. Under such conditions, OM decomposition is very slow, leading to the accumulation of undecomposed debris in the organic layers, although decomposition might be enhanced in the Ah horizons, once the conditions become more eutrophic. On the other hand, in the AMP soils, both lithology and plant species have a clear effect on the type of pedogenesis occurring in the surface horizons. The results show that the pine stand is able to produce greater surface acidification (although never as intense as that on GR materials) than in the eucalypt and the oak litter. In general, the eutrophic conditions of these soils allow rapid decomposition of primary OM. The geochemical conditions of the surface mineral horizons appear to allow neoformation of metastable forms of gibbsite and different short-range order 1:1 aluminosilicates, which may bind to secondary organic compounds. Under such conditions, decomposition of secondary OM is slowed down.

Aboveground Biomass, Belowground Biomass and Dead Wood

As indicated above, the estimates of the organic C stocks for each of the reservoirs per unit of surface (t ha^{-1}) down to the lowest depth of the Ah horizons (Figure 5) indicate that organic C in SOM was always higher than the amount of organic C in living biomass, with the highest (82%) and lowest (50%) relative values of SOM corresponding to the eucalypt stands (Figure 4). The relative amounts of soil organic C for the pine and oak stands were very similar (ranging from 65 to 70%), independently of the parent material. The fact that eucalypts are managed more intensively than the other species (they are managed in rotation periods of 10-15 years, with heavy machinery used for harvesting and site preparation) may have a variable impact on the SOM stock and this may explain the large differences observed in the eucalypt stands. The accumulation of SOM is a slow process, which can be interrupted by practices such as clear cutting (Constantini et al., 1991), and the use of heavy machinery.

The latter practice has similar effects on SOM as cultivation, as it leads to disruption of soil aggregates, which favours mineralization of the occluded labile SOM (Plante et al., 2006). Both practices may also lead to greater fluctuations in temperature and moisture (no canopy is present) with subsequent increased SOM mineralization, and furthermore to increased erosion, with the concomitant loss of SOM. In any case, it should be noted that the highest total organic C stocks, i.e., the sum of the five reservoirs considered, always corresponded to the eucalypt stands (Figure 4), with stocks above 500 t ha^{-1}, whereas the oak and pine stands had stocks below 500 t ha^{-1}, and when comparing each forest species between the two types of ecosystems, the total organic C stocks were systematically greater in the AMP than in the GR ecosystems.

Apart from the inherent species characteristics (fast growth - eucalypts; medium-speed growth – pines, and slow growth - oaks), the different management regimes applied to the different species may also have an important impact on the biomass C pools present in the studied stands. Oaks are managed as a coppice, and the density of trees is very high (AMP-O: 2340; GR-O 3150 trees ha^{-1}), with many trees of small diameter (average diameter; AMP-O: 12.4; GR-O: 5.3 cm). However, clear differences were observed between the two eucalypt stands studied. The fast-growing eucalypts showed a high proportion of organic C in the aboveground biomass pool in the GR stand (34%), whereas there was very little organic C in the biomass from the AMP site (9%), which is probably attributable to the age difference (8 compared with 13 years) and to several severe attacks by *Gonipterus scutellatus* Gyllenhal in AMP-E in recent years. Attacks by the insect generally cause severe reduction in production. The relative amounts of organic C in the aboveground biomass of oak and pine stands were very similar (ranging from 15 to 18%). The dead wood (standing and on the floor) present in both oak stands showed high relative values (>1%) (Figure 4). Despite the small diameters, this may also be very important for biodiversity. The AMP-P plot is an old and abandoned pine plantation and the tree density is therefore low (< 350 live trees ha^{-1}, including new regeneration) and there is a considerable amount of dead wood for a commercial plantation (18 Mg C ha^{-1}; >3% of the total C stock). Finally, GR-P is a younger well-managed pine plantation with no dead wood.

CONCLUSION

The results obtained indicate that highest total organic C stocks in the ecosystems studied down to the lowest depth of the Ah horizons, i.e., the sum of the five reservoirs considered, always corresponded to the eucalypt stands, with stocks > 500 t ha^{-1}, whereas those of the oak and pine stands were always < 500 t ha^{-1}. The mean distribution of organic C stocks in the five reservoirs considered was as follows: aboveground biomass, 18.4%; belowground biomass 4.6%; dead wood, 1.1%; litter 8.4%; and soil organic C, 67.2%, with no significant differences ($P < 0.05\%$) between means for the AMP and GR ecosystems, although for each type of forest species, total C stocks were consistently higher in the AMP than in the GR ecosystems. There were significant differences ($P<0.05$) in the quantity, quality and dynamics of organic C of these two types of ecosystems, when the different organic layers (L and F) and also the different Ah horizons (Ah1 and Ah2) were considered separately.

To understand the possible mechanisms of OM stabilization taking place in the organic layers and Ah horizons of the soils under study, the processes involved in pedogenesis must be understood. For this, we could consider the incipient formation of an acid soil in a humid and percolating environment as a titration of the primary parent material against an excess of organic acids ultimately derived from the biomass (Camps Arbestain et al., 2007; Macías et al., 2007). The net release of acid breaking products from organic debris is mainly affected by environmental conditions (favoured when microbial activity is impaired) and type of vegetation, whereas the acid buffering capacity of the parent material is mainly affected by lithology and/or climate (Camps Arbestain et al., 2007; Macías et al., 2007). The shifting point of this titration, which depends on both the total organic acid loading and the base supplied, determines whether downward movement of organic acids takes place, and if this occurs, at what depth the movement stops, with the formation of new phases.

During incipient weathering of amphibolites under humid temperate conditions in a percolating environment, rapid dissolution of Si, Al, Fe, and non-hydrolyzing cations (e.g., Ca, Mg) from primary minerals takes place. Large quantities of the latter are removed via leaching, whereas Al, Fe, and to a lesser extent Si, are retained preferentially, producing rapid buffering of the organic acid loading, and there being almost no downward movement of complexing organic acids. In these soils, solubilization of primary minerals takes place at a faster rate than crystallization of secondary minerals, leading to formation of meta-stable short-range order compounds, such as allophane and imogolite, together with stable organo-metal complexes, which increases both the sorption properties of these soils and water retention. Moreover, the base supply from major primary minerals favours the existence of eutrophic conditions, and the pH of the system is maintained in the range of acid-hydrolysis, and is mainly controlled by dissolved CO_2. All of this favours OM decomposition and the bonding of the metabolized organic compounds with reactive Al surfaces. Under such conditions, decomposition of secondary OM is slowed down, and this process is could be further retarded by the high water content capacity of these soils, as proposed by Buurman (2006) for allophanic Andosols under perudic conditions, although more research is required to confirm this. All this explains the accumulation of soil OM in natural soils with andic properties.

On the other hand, incipient weathering of granite rocks under humid temperate conditions in a percolating environment drastically eliminates the scarce bases present in the GR parent material, leading to a more acidic system. At the surface there is practically no mineral stability, and the pH of the system is mainly determined by biogeochemical processes. Under such conditions, the acidity produced through the release of organic acids cannot be totally buffered by mineral alkalinity, and the solubility of Al and Fe becomes determined by complexation reactions, with the formation of aqueous organo-mineral complexes, which can be transported to deeper layers (e.g., from organic horizons to mineral surface horizons, such as the Ah horizons) until they become saturated and precipitate. This situation corresponds to strong acid-complexolysis under highly dystrophic conditions in the litter layers where decomposition of organic debris is slow and primary OM tends to accumulate, although decomposition which be enhanced in the Ah horizons, once the conditions become more eutrophic. This may explain the existence of a moder-type OM in the former in comparison with the Al-mull type of OM in the latter. However, in spite of these differences, estimated losses of organic C in the Ah1 horizons of forest soils converted to agricultural use were similar in both type of soils (despite the well-known ability of soils with andic properties to accumulate OM under natural conditions), and indicates the vulnerability of both types of OM to being depleted when they are subject to conventional agricultural practices.

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Chapter 6

THE ORIGINAL ECONICHE OF THE GENUS *HOMO*: OPEN PLAIN OR WATERSIDE?

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ABSTRACT

That humans evolved as a result of a move from forests to more open plains is still the prevailing paradigm in anthropology, and researchers often assume that this transition influenced the origins of human bipedalism, omnivory, tool use, large brains, and even speech. Here, we argue that there are no scientific grounds on which to base such a hypothesis. While we agree that *Homo* may have evolved in more open (tree-poor) habitats than other apes (which could account for our relatively poor climbing skills), the suggestion that humans shifted to drier habitats away from water is, according to our

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research, unproven. We propose instead a more parsimonious model compatible with all known data and corroborated by a number of independent sources of evidence.

Comparisons of the locomotor styles and nutritional requirements of extant species and anatomical comparisons of fossil and extant species including *Homo sapiens*, especially in combination with palaeoecological data, strongly suggest that early *Homo* evolved at the water's edge (whether in savannahs or elsewhere) where resources essential for brain growth were both abundant and easily procurable by a thick-enameled tool-using omnivorous hominid.

INTRODUCTION

Many anthropologists still essentially follow the 20th-century view, exemplified by Dart (1925), that "a vast open country with occasional wooded belts and a relative scarcity of water" furnished the conditions that were necessary for the evolution of naked, bipedal, large-brained humans. Recent models, when taken together, suggest that *Homo* may have acquired a larger brain because, through endurance running, it was able to out-compete other savannah dwellers for scavenged carcass remains in open, semi-arid environments, thus providing access to the extra fats and proteins required for increased brain growth (e.g., Cordain *et al*. 2001, Bramble and Lieberman 2004).

The 'endurance running' model is one of the latest of a long list of anthropological models that conform to the idea that a shift in econiche from forests to more open landscapes was primarily responsible for the evolution of the genus *Homo*. These models have been collectively labelled 'open plain' hypotheses (Bender 1999). These hypotheses offer easy-to-understand scenarios for human origins, and were formulated well before most fossil hominid evidence had been discovered (Bender 1999). They were based from the very beginning on unproven assumptions rather than solid evidence, yet they today remain the dominant paradigm in human evolution in mainstream popular culture (see, e.g., the BBC productions *Walking with Cavemen*, and David Attenborough's *Life of Mammals* which, although acknowledging that human bipedalism may have evolved through wading, typifies *Homo* as long-distance 'persistence' hunters who run their prey down) and in respected peer-reviewed journals (e.g., Langdon 1997). Possibly, the strong (either implicit or explicit) tendency to regard humans as unique might explain why these 'open plain' ideas were never ecologically tested and methodically scrutinised. This tendency could also perhaps explain why traditional anthropology places remarkably little value on comparative biological data: if our species is 'unique', why would one expect to see parallels with other animals?

This anthropocentric perspective is contrary to the way we approach human evolution in this Chapter. We believe one of the key ways to understand human evolution is by comparing our species to other species: if something is true for other species, there is no *a priori* reason why this could not also be true for humans. We also believe that traditional human evolutionary models place too little emphasis on the broader topic of hominoid evolution (for instance, how the human–chimpanzee last common ancestor lived, and how the African apes evolved), whereas in our view this is essential. Although innumerous facts contradict the savannah and 'endurance running' models, it seems 'open plain' thinking is simply too traditional, widespread and 'self-evident' to be easily dropped.

In this Chapter, we argue that ‘open plain’ models are incompatible with otherwise widely accepted concepts in evolutionary biology such as gradualism and convergence, and that they fail to take into account comparative biology. We present old and new scientific evidence contradicting ‘open plain’ interpretations and/or supporting more parsimonious ‘waterside’ models. Unlike ‘open plain’ models, waterside models are based primarily on comparisons with other animals.

We present nutritional, behavioural, anatomical, locomotor and palaeoecological data which indicate that *Homo* populations have always (apparently at least until the late Pleistocene) lived at the water’s edge, where they could have collected a variety of foods from trees, from shores and from below the water’s surface. These waterside ecological niches could help explain peculiarities in which humans differ from other primates, such as loss of fur, abundant subcutaneous fat tissues, alined body posture, well-developed dexterity and a large brain – characteristics typical of mammals which inhabit aquatic and littoral habitats, but rare in cursorials and arid adapted animals.

‘OPEN PLAIN’ HYPOTHESES IN ANTHROPOLOGY

> “… It will appear to many a remarkable fact that an ultra-simian and pre-human stock should be discovered, in the first place, at this extreme southern point in Africa, and, secondly, in Bechuanaland, for one does not associate with the present fringe of the Kalahari desert an environment favourable to higher primate life. It is generally believed by geologists (*vide* A. W. Rogers, ‘Post-Cretaceous Climates of South Africa,’ *African Journal of Science*, vol. xix., 1922) that the climate has fluctuated within exceedingly narrow limits in this country since Cretaceous times. … For the production of man a different apprenticeship was needed to sharpen the wits and quicken the higher manifestations of intellect – a more open veldt country where competition was keener between swiftness and stealth, and where adroitness of thinking and movement played a preponderating role in the preservation of the species. Darwin has said, no other country in the world abounds in a greater degree with dangerous beasts than Southern Africa, and, in my opinion, South Africa, by providing a vast open country with occasional wooded belts and a relative scarcity of water, together with a fierce and bitter mammalian competition, furnished a laboratory such as was essential to this penultimate phase of human evolution. …”

This is an extract from Professor Raymond Dart’s (1925) famous paper, ‘*Australopithecus africanus*: the man-ape of South Africa’, published in *Nature* shortly after the discovery of the first australopithecine fossil, the ‘Taung child’. Following the geological view of his time, Dart argued that the ancestors of man, for Dart saw the Taung child as a representative of early human ancestors, must have lived in treeless grasslands similar to the habitat in which the Taung skull was discovered. There is good evidence today, however, that the South African climate has changed drastically over time, and that the Taung child probably inhabited not treeless grasslands, but wet, tropical forests (e.g., Partridge 1985).

Dart was merely following the ‘open plain’ ideas that were particularly popular in the early 1900s (‘*Freilandhypothesen*’, see Bender 1999), and which go back almost two hundred years (e.g., Lamarck 1990: 261, Reinhardt 1906: 6, and Arldt 1907: 606). These hypotheses were based upon two facts and one subjective interpretation of these facts (see Figure 1).

The differences between humans and apes, the traditional story suggests, came about because humans left the forests and adapted to living on open plains (Bender and Oser 1997). The first primates were quadrupedal arboreals living in forests (most primates), and later they evolved into bipedal terrestrials living outside forests (humans), so therefore bipedalism must have evolved because human ancestors left the forests. But while this might seem an obvious conclusion, it is in fact a logical fallacy of the type: *post hoc, ergo propter hoc* ('after that, therefore because of that'), and our comparative research suggests to the contrary that there is no evidence that the two (leaving the trees and becoming bipedal) are causally related: in fact, ground-dwelling and savannah primates such as patas monkeys and hamadryas baboons are *more* quadrupedal than forest and arboreal primates such as indris, tarsiers, proboscis monkeys and gibbons.

'Out of Eden' hypotheses, which dominated thinking in the early 20th century, contrasted luxurious tropical forest econiches characterised by easy fruit-picking with a tough hunting life on open plains outside the forest, which required large brains, speech, and bipedality to 'free the hands' so that they could be used for holding tools and weapons. As Abel (1931: 369) pointed out, these early 'open plain' hypotheses were situated in many different locations, including India, Indonesia, Australia, Africa and Europe, and occurred anywhere between thirty million years ago to only a few hundred thousand years ago. As an historical analysis showed, the same sequence of events was always emphasised: the transition from a 'lower' apelike animal lifestyle towards the 'higher' human lifestyle characterised by mastering of the environment, whereever or whenever they were situated (Bender 1999: 75-79).

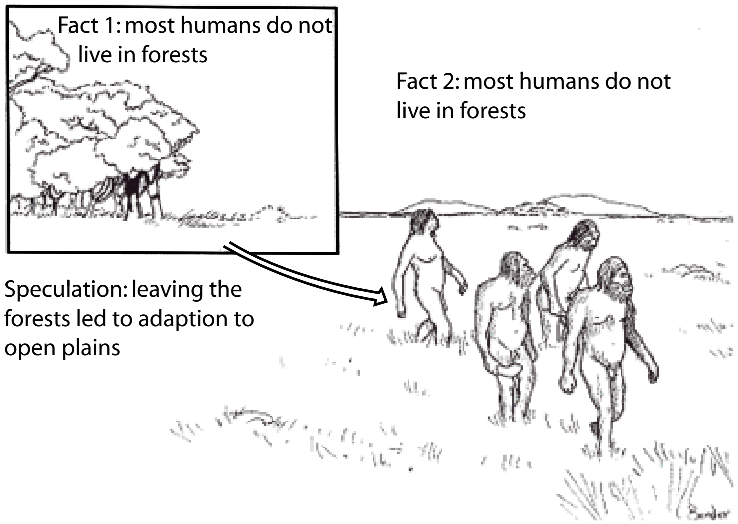

Figure 1. Origin of the 'open plain' hypotheses. Early scientists speculated from Fact 1 ("most primates live in forests") and Fact 2 ("most humans do not live in forests") that a transition from life in the woods to life on open plains was essential to the evolution of human characteristics such as bipedalism (adapted from Bender-Oser 2004).

Table 1. Four main episodes included in orthodox human evolutionary models (Landau 1984)

Episode	Description
Terrestriality	A shift from the trees to the ground
Bipedalism	The development of upright posture
Encephalisation	The development of the brain, intelligence, and language
Civilization	The development of technology, morals and society

Landau (1984), after studying texts on human evolution written by early 20th century scientists Arthur Keith, Grafton Elliot Smith, Frederick Wood Jones, Henry Fairfield Osborn, and William King Gregory, concluded that, “there appears to be some underlying agreement about what happens in human evolution. In constructing their theories, most anthropologists seem to have in mind a similar narrative pattern.” These narratives had four main episodes (Table 1), one of which was “a shift from the trees to the ground (terrestriality)” (1984: 264, see also Landau 1991).

The narrative style, Landau discovered, was overall most similar to popular folk-tales in which heroic characters, when faced with adversity, overcame great odds to prevail. While there was room within these narratives for different chronologies (bipedalism might have occurred before or after terrestriality, for example), the four key episodes were always included, thus forming a somewhat predictable framework. Perhaps this is why waterside models never made an impression in the minds of most anthropologists. In waterside models, there is no shift from the trees to the ground (episode of terrestriality), these models therefore fail to conform to the prevailing narrative framework, and are consequently considered unorthodox and ‘impossible’.

Later in the 20th century, scenarios no longer based solely on the courage or initiative of early human ancestors were proposed, and these stressed instead the importance of external factors such as climatic changes, which led to shrinking forests and expanding open plains, notably, the dry and hot East-African savannahs (see especially Dart 1925, and for more recent discussion deMenocal 2004). This process of aridification more or less ‘forced’ our arboreal ancestors to leave the forests and expand into more open, arid habitats (discussion in Bender 1999: 56-59, see Figure 2).

Anthropologists often assume that this shift from ‘internal’ factors (human courage, curiosity, intelligence) to ‘external’ factors (climatic or geological changes which caused aridification and/or deforestation) came about because of the discovery of fossils and artefacts in areas that could only have been open savannah, but a survey of the literature shows that *Homo* sites are typically found near large water bodies including rivers, lakes, swamps and coasts, and not necessarily in open savannahs (see below).

Dart’s version of the ‘open plain’ hypothesis eventually became widely accepted, mostly after the Piltdown debacle had been uncovered. The Piltdown hoax, in which an orangutan mandible and a modern human cranium were fraudulently buried and altered so that they appeared to belong to the same fossil species, was accepted as a genuine human ancestor for a number of years (1912–1940). Schematically, therefore, the consensus view at the time of Piltdown was that human ancestors had large canines and a large brain. When the hoax was becoming apparent, it also became clear that a new scheme was required, and eventually scientists supported the opposite view (Lewin 1987: 60-84, Le Gros Clark 1955), accepting Dart’s Taung skull (small canines, small brain) as the intermediate step between apes (large canines, small brain) and humans (small canines, large brain).

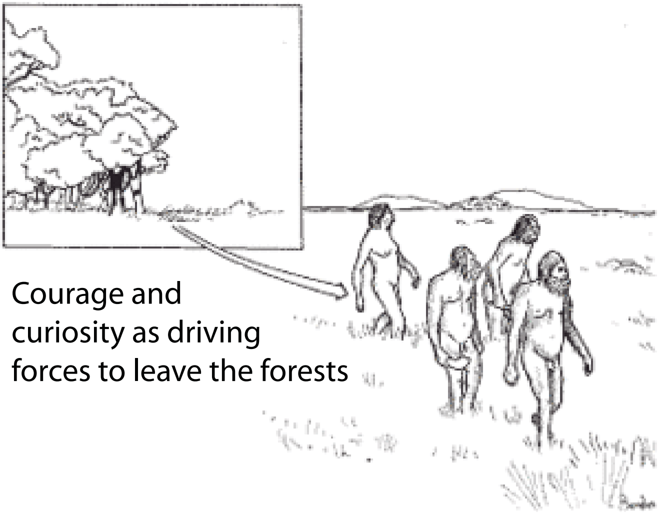

Figure 2a. Early ‘open plain’ hypotheses stressed mostly internal factors such as courage or curiosity to explain the transition from forests to open plains (adapted from Bender-Oser 2004).

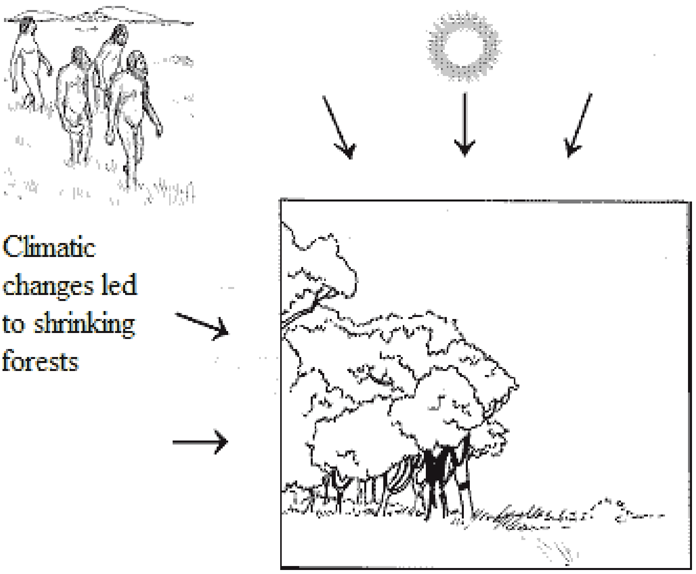

Figure 2b. Later, ‘modern’ versions began to stress more and more ‘external factors’ such as climatic factors and shrinking forests to explain this transition (adapted from Bender-Oser 2004).

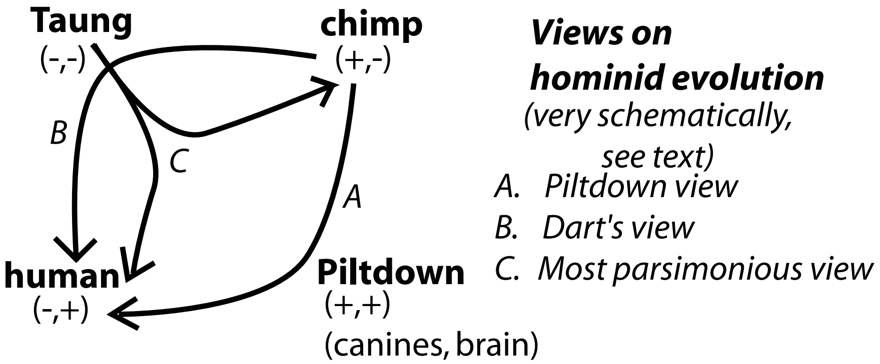

Figure 3. Different views on hominid evolution, very schematically (see text).
A. View based upon the fraudulous Piltdown skull. Large-toothed, small-brained apelike ancestors (+,-) evolved via large-toothed, large-brained Piltdown-like intermediates (+,+) into small-toothed, large-brained humans (-,+).
B. Traditional view after accepting the Taung fossil as a 'hominid', diametrically different from the Piltdown view. Apelike ancestors (+,-) evolved via australopithecines, exemplified by the Taung skull (-,-), into humans (-,+). In both tradiational views (A and B), 'apelike' equals 'primitive'.
C. Alternative view incorporating temporal data: older specimens are more likely to have more primitive characteristics (Fox *et al*. 1999). It does not intend to say that both humans (-,+) and chimpanzees (+,-) descend from Taung, but rather that both evolved in different directions from more australopith-like ancestors (-,-) and that both humans and chimpanzees have several derived features (e.g., Drapeau and Ward 2007).

In the view of three of us (for the view of RB and NB, see Bender 1999), the Taung skull is not an intermediary between an ancestral apelike and an extant humanlike skull (the view that many palaeoanthropologists today tend to adopt). Instead, we prefer the more parsimonious views that evolutionary changes happened in both lineages (*Homo* as well as *Pan*) rather than that nearly all evolutionary changes happened in one lineage (*Homo*) and that the older skull is nearer to the ancestors of the living species (Fox *et al*. 1999), so that both chimpanzees and humans had more australopithecine-like ancestors (for detailed arguments, see Verhaegen 1994, 1996) (Figure 3).

Significantly, when, in the 1940s and 1950s, most palaeoanthropologists rejected Piltdown, not only did they accept Dart's ideas on Taung being ancestral to humans, but also his views on where it might have lived ("a vast open country with … a relative scarcity of water"), which we now know (e.g., Partridge 1985) were based on incorrect conclusions.

A Diversity of 'Open Plains' Ideas

The original 'open plain' ideas were obviously hypothetical, but soon the general impression of human ancestors coming out of the trees and colonizing the vast plains became set in the minds of most anthropologists, and different ideas – some more improbable than others – were put forward to explain how savannah-dwelling ancestors might have found enough food and water to survive on the open plains – as if the hypothesis had already been proven. Human characteristics were discussed in an evolutionary setting that involved a movement from the forests to the open plains, and reasons for these characteristics always tended to revolve around the ‘open plain’ theme (see Table 2). Even the most far-fetched of these ideas (for example, honey collection, liver consumption, or food collection at noon on open plains) have been seriously considered and published in scientific journals. Such *ad hoc* explanations are comparable to the hypothetical ‘land bridges’ between Africa and South-America that were popular in geology before the theory of Plate Tectonics became accepted.

What is striking about these hypotheses is their combined diversity. Some rely on hunting large game, others on small game, some on scavenging bone marrow, or brains, or livers, or collecting seeds, or tubers, or honey. Some of these ‘open plain’ models are more typical of slow-moving animals (feeding on belowground resources), others of fast-moving mammals (“bouts of strenuous activity”), and others rely on endurance (following migrating ungulates, or the dogged pursuit of prey). This diversity of theoretical models suggests that the ‘open plain’ scenarios are not the result of usual biological thinking. In evolutionary biology, hypotheses are not just ‘possible scenarios’, but normally the result of solid analyses of relationships between form and function. Biologists usually do not propose a scenario to explain the evolution of an animal without a careful comparison of different features of this animal with similar features (*convergences*) of other, not closely related species.

Table 2. Diverse savannah hypotheses of human origins.

Raymond Dart 1960	Osteodonto-keratic Culture – Savannah hunting
Robert Ardrey 1961	Man the Mighty Hunter – African Genesis – Adult men hunting large game
Mikhail Nesturkh 1967	Herd instinct developed along with bipedalism as our ancestors moved to more open territory.
Desmond Morris 1967	Mighty Hunter – The Naked Ape – Fur loss for easier sweating
Clifford Jolly 1970	The Seed Eaters – Savannah baboon model
John Napier 1971	Open grassy spaces provided ‘arenas’ where new locomotor skills could be safely practiced.
Hatley & Kappelman 1980	Belowground food resources
Walker, Zimmerman & Leakey 1982	High dietary intake of carnivore livers – Scavenger model
Hanna & Brown 1983	Bouts of strenous activity for hunting or digging outside the forest
Peter Wheeler 1984	Savannah foraging at noon, to minimise solar radiation
David Carrier 1984	Dogged pursuit of swifter animals over 1 or 2 days
Sinclair, Leakey & Norton-Griffiths 1986	Bipedal trekking after herds of migrating ungulates
Mark Skinner 1991	Savannah bee brood consumption – Tall grass savannah & tropical forest
Richard Wrangham *et al.* 1999	Cooking and bringing food to a processing area
Bramble & Lieberman 2004	Endurance Running over vaste plains
Dennell & Roebroeks 2005	Ability to ingest large amounts of meat – ‘Savannahstan’
Richard Wrangham 2005	Delta hypothesis – Okavango-like savannah – Omnivory

Whereas modern biology sees evolution as a *sequence of overlapping niches* (Kemp 2007), the proposed 'open plain' lifestyles of these early human ancestors are discontinuous and have little or no overlap. Frequently they are incompatible with each other. Moreover, they suppose that humans collected foods without the typical adaptations that other mammals use when they collect the same foods. We have no large digging-claws, for example, we are slow runners (only some 36 km/hr over short, and some 20 km/hr over long distances), and we are very prone to dehydration by depletion of water and salts. We are heavily-built creatures with extensive fat tissues and (in archaic *Homo*) heavy bones, features that are not seen in cursorial species. Our cheekteeth lack the seed-grinding adaptations of baboons, while the human gastro-intestinal tract and digestive anatomy and physiology resemble frugi-omnivores such as suids, not carnivorous mammals (Stevens 1990). This contradiction has been labelled the 'baboon paradox', because we would expect humans to be more similar to baboons if we evolved on the savannah as they apparently did (Bender 1999).

The collection of waterside food resources, on the other hand, is compatible with the presumed lifestyle of early apes, and fits with modern human food-gathering strategies. Shifting from a fruit-based diet to a diet including more waterside foods such as coconuts and shellfish does not require significant behavioural modification. The use of tools to open hard-shelled nuts and fruits is easily transferable so that the meat of certain molluscs can also be procured (capuchin monkeys use tools to open fruit, nuts and shellfish), and shellfish, like fruits and nuts, are sessile food resources that need only be found and gathered, not chased or hunted. From such fruit, shellfish, plant and egg-gathering it is not difficult to envisage the incorporation of waterside catching of insects, frogs, fish or birds, and the butchering of turtles, crabs, whale or bovid carcasses found at the water's edge. We do not claim to know exactly how this waterside lifestyle evolved, but we are confident that the limited diving skills of humans came about as a result of increased time spent foraging under water. As to how frequently our ancestors may have dived or waded or collected fruit from trees or foods along the shore at low tide, or how long our ancestors' waterside phase or phases may have lasted, these are all questions requiring further investigation.

Questioning the Savannah Model

Although the savannah model still dominates anthropological thinking, many leading palaeoanthropologists no longer follow it automatically (Table 3). No other than professor Phillip Tobias, Dart's mental heir, already an emeritus himself, recently stated that "… All the former savannah supporters (including myself) must now swallow our earlier words in the light of the new results from the early hominid deposits ... Of course, if savannah is eliminated as a primary cause, or selective advantage of bipedalism, then we are back to square one. …" (Tobias 1995, 1998).

This questioning of the savannah model (Table 3) resulted from two lines of evidence: firstly, palaeoecological studies showed that the earliest bipedal hominids were associated not with open plains, but with wooded or forested environments (e.g., Tobias 1998); and secondly, anatomical studies showed that australopithecines and early *Homo* species such as *habilis* had good climbing abilities (e.g., Collard and Wood 1999) (some of which persisted into *Homo georgicus* and possibly even *Homo floresiensis*, see Lordkipanidze *et al.* 2007, and Tocheri *et al.* 2007). Rather than abandon the savannah theory, however, the chronology of events has been rearranged, with *Homo erectus* now seen as the first true savannah hominid, descending from earlier australopithecine and *habilis*-like species that are now seen as adapted to mosaic habitats including both forests and open plains (see Langdon 1997).

Table 3. Some quotes of leading palaeoanthropologists doubting savannah hypotheses

Tobias 1995	"We were all profoundly and unutterably wrong! … All the former savannah supporters (including myself) must now swallow our earlier words …"
Wood 1996	"the 'savannah' hypothesis of human origins, in which the cooling begat the savannah and the savannah begat humanity, is now discredited"
Stringer 1997	"One of the strong points about the aquatic theory is in explaining the origin of bipedality. If our ancestors did go into the water, that would forced them to walk upright …"
Tobias 1998	"Bamford identified fossil vines or lianas of *Dichapetalum* in the same Member 4: such vines hang from forest trees and would not be expected in open savannah. The team at Makapansgat found floral and faunal evidence that the layers containing *Australopithecus* reflected forest or forest margin conditions. From Hadar, in Ethiopia, where 'Lucy' was found, and from Aramis in Ethiopia, where Tim White's team found *Ardipithecus ramidus* … well-wooded and even forested conditions were inferred from the fauna accompanying the hominid fossils. All the fossil evidence adds up to the small-brained, bipedal hominids of four to 2.5 Ma having lived in a woodland or forest niche, not savannah." "… if ever our earliest ancestors were savannah dwellers, we must have been the worst, the most profligate urinators there"
Stringer 2001	"In the past I have agreed that we lack plausible models for the origins of bipedalism and have agreed that wading in water can facilitate bipedal locomotion (as observed in other normally quadrupedal primates). I have never said that this MUST have been the forcing mechanism in hominids, but I do consider it plausible. As for coastal colonisation, I argued in my *Nature News & Views* last year that this was an event in the late Pleistocene that may have facilitated the spread of modern humans."
Groves & Cameron 2004	"Nor can we exclude the Aquatic Ape Hypothesis. Elaine Morgan has long argued that many aspects of human anatomy are best explained as a legacy of a semiaquatic phase in the proto-human trajectory, and this includes upright posture to cope with increased water depth as our ancestors foraged farther and further from the lake or seashore."
Wrangham 2005	"Here I follow the conventional assumption that hominins began in the savanna." "… the composition of the Okavango as a network of islands could favor the evolution of bipedalism. For those who envisage bipedalism as facilitated by the need to traverse or exploit aquatic environments, an inland delta that generates low islands termitogenically or hydrodynamically offers rich scenarios."
Alemseged 2006	"I believe we should just put the savannah theory aside. I think they basically became biped while they were living in a wooded, covered environment …"
Thorpe *et al*. 2007	"… early hominins occupied woodland environments, not open or even bush-savannah environments (such as sites including Allia Bay, Aramis, Assa Issie and now Laetoli) ... they retained long grasping forelimbs, which are more obviously relevant in an arboreal context…"

Below we discuss anatomical, physiological, dietary and palaeoecological data indicating that a waterside lifestyle for our direct ancestors is many times more plausible as an explanation for our mental and physical characteristics than any ‘open plain’ or savannah-based hypotheses, and that *Homo erectus* was more likely to have been a waterside specialist than an arid savannah specialist. As an illustration, we compare the recently outlined ‘endurance running’ model with a model that includes part-time waterside dwelling as a prerequisite to later evolution of terrestrial bipedalism. Note that while Wrangham (2005) includes part-time waterside dwelling to explain the evolution of australopithecines, he still follows “the conventional assumption that hominins began in the savannah.”

Endurance Running or Littoral Locomotion in Archaic *Homo*?

Bramble and Lieberman (2004), in a much-discussed review article in *Nature*, cite a number of derived *Homo* features they claim to be adaptations for more efficient endurance running in arid, open habitats. However, while some of these supposedly ‘cursorial adaptations’ appear first in the fossil record in *H. habilis*, others appear first in *H. erectus*, and others still in *H. sapiens*, suggesting a much more complex story than proposed by Bramble and Lieberman. Their conclusions are reached without systematic comparisons with other animals (including endurance runners) and with general comparisons restricted to fossil hominids and *Pan*. Since convergent traits are strong indicators of evolution in similar environments (Bender 1999), a systematic comparison with a broad range of animals with a variety of locomotor strategies would have been more informative.

In addition, discussion of possible locomotion styles is restricted to walking and running, with no consideration at all given to activities such as wading, swimming or underwater foraging, yet humans are regular waders and more accomplished swimmers and divers than other primates. Most of the list’s ‘adaptations’ for walking could just as easily be explained by wading. One of the frequent ‘explanations’ in the list is “stress reduction”, a reference to the vertical posture of humans with the weight resting on two legs. But this says nothing about endurance running, with standing, wading, walking or short distance running all using a similar posture, and therefore all requiring stress reduction. Other ‘explanations’ include “counter rotation”, “thermoregulation” and “stabilization”, but no comparative data to corroborate these interpretations are provided. In other words, their ‘explanations’ are *ad hoc* suppositions, applied to one example (human ancestors) without any consideration as to whether these supposed adaptations are seen in other animals, which means their ‘explanations’ are statistically invalid (n=1). Long legs, and possibly shortened forearms, could be seen as running adaptations, but these are just as typical of wading and swimming species compared with runners (Hildebrand 1974: 584, Bender 1999).

In a waterside scenario, wading and swimming would be preadaptative to the humanlike ‘vertical’ locomotion that Bramble and Lieberman (2004) believe to be a direct adaptation to endurance running. In our view, frequent terrestrial locomotion, whether for walking or for (relatively slow) running, was more recent (*Homo sapiens*) and could not be derived directly from an ancestral locomotion in forests, whether on the ground or in the branches, because in that case a more baboon-like locomotion would be expected (the ‘baboon paradox’).

Table 4. Bramble and Lieberman's (2004) list of supposedly derived features of the human skeleton with so-called cursorial functions

	Functional role in running & walking according to Bramble & Lieberman (2004)	W = walk R = run	Earliest evidence	Comparative data. More likely alternatives in our opinion. NSS = not seen in savannah animals. NSC = not seen in cursorial animals. NUL = not unexpected in littoral animals.
Enlarged posterior & anterior semicircular canals	Head/body stabilization	R	*H. erectus*	NSS as far as known. NUL, e.g., for equilibrium during descent & ascent in diving. Requires more comparative data.
Expanded venous circulation of neurocranium	Thermoregulation	R>W	*H. erectus*	NSS. NSC. NUL. Skull base & paravertebral venous networks are typical of diving species.
More balanced head	Head stabilization	R	*H. habilis*	NSS. NSC. Could be advantageous in frequent standing rather than running. Alined build NUL.
Nuchal ligament	Head stabilization	R	*H. habilis*	NUL, e.g., in pronograde swimming.
Short snout	Head stabilization	R>W	*H. habilis*	NSS. NSC. Snout shortening has to do with mastication rather than head stabilisation.
Tall, narrow body form	Thermoregulation	R>W	*H. erectus*	NUL: long legs are typical of wading species.
Decoupled head & pectoral girdle	Counter-rotation of trunk *vs* head	R	*H. erectus*?	NUL: waterside as well as a mosaic milieus require versatile locomotions.
Low, wide shoulders	Counter-rotation of trunk *vs* hips	R	*H. erectus*?	NUL: 'low' could be for wading as well as for underwater swimming. No relation to running.
Forearm shortening	Counter-rotation of trunk	-	*H. erectus*	NUL: typical of frequently swimming species.
Narrow thorax	Counter-rotation of trunk *vs* hips	R	*H. erectus*?	Dorso-ventrally narrow. NSS, NSC, NUL: typical of shallow water dwellers, e.g., platypus, hippo, beaver.
Narrow & tall waist between iliac crest & ribcage	Counter-rotation of trunk *vs* hips	R	*H. erectus*?	NUL: waterside as well as mosaic milieus require a wide range of locomotions.
Narrow pelvis	Counter-rotation of trunk *vs* hips Stress reduction	R R>W	*Homo*?	*H. erectus* had still flaring ilia, presumably for femoral abduction: NSS, NSC, NUL.

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	Functional role in running & walking according to Bramble & Lieberman (2004)	W = walk R = run	Earliest evidence	Comparative data. More likely alternatives in our opinion. NSS = not seen in savannah animals. NSC = not seen in cursorial animals. NUL = not unexpected in littoral animals.
Expanded lumbar central surface area	Stress reduction	R>W	*H. erectus*	Suggests vertical body. NUL, e.g., for wading.
Enlarged iliac pillar	Stress reduction	R>W	*H. erectus*	Idem.
Stabilized sacroiliac joint	Trunk stabilization	R	*H. erectus*	Idem.
Expanded surface area for mm. erector spinae origin	Trunk stabilization	R	*H. erectus*	Idem.
Expanded surface area for m. gluteus maximus origin	Trunk stabilization	R	*H. erectus*	Idem.
Long legs	Stride length	R>W	*H. erectus*	NUL, typical of wading species.
Expanded hindlimb joint surface area	Stress reduction	R>W	*H. erectus*	Suggests vertical body. NUL, e.g., for wading.
Shorter femoral neck	Stress reduction	R>W	*H. sapiens*	Not seen in *H. erectus*. Presumably post-littoral.
Long Achilles tendon	Energy storage Shock absorption	R	*Homo*?	Comparative data are needed. Typical cursorial species are not plantigrade. NUL.
Plantar arch (passively stabilized)	Energy storage Shock absorbtion Powered plantar-flexion	R R>W R>W	*Homo*?	NSS. NSC. NUL: plantigrady for wading and swimming.
Enlarged tuber calcaneus	Stress reduction	R>W	*Homo*?	Cursorials do not have enlarged heels. NSS. NSC. NUL.
Close-packed calcaneo-cuboid joint	Energy storage Stability during plantarflexion	R>W	OH-8	Comparative data are needed. NUL.
Permanently adducted hallux	Stability during plantarflexion	R>W	OH-8	NUL: wading, swimming.
Short toes	Stability during plantarflexion Distal mass reduction	R>W	OH-8	NSS. NSC. NUL: metatarsal lengthening and toe shortening is to be expected in swimming & wading.

Most of Bramble and Lieberman's 'adaptations' are not what we would expect in a cursorial (running) animal. For example, their list includes "enlarged posterior and anterior semicircular canals", but there are no comparisons with, for instance, giraffes (heads high above the ground), gibbons (fast and versatile locomotion), kangaroos (cursorial bipeds), or swimming or diving species. It is conceivable in fact that the frequent change of posture seen when diving for seafood (descending and ascending) required a different labyrinth structure, and that the *Homo erectus* labyrinth was adapted to terrestrial walking and running as well as to wading, swimming and diving locomotions.

There is no indication that an "expanded venous circulation of neurocranium" had anything to do with thermoregulation, but there is long-standing evidence of expanded venous networks in diving species (Slijper 1936).

More balanced heads and short snouts are not seen in cursorial species, whether bi- or quadruped, and low shoulders are to be expected in wading and underwater swimming.

What Bramble and Lieberman refer to as "narrow body form", "narrow thorax" and "narrow pelvis" is not clear to us: compared to most primates, humans have a relatively broad thorax and pelvis (laterolaterally), and this was even more so in the case of australopithecines. In our opinion, the combination of 'flared' iliac blades and long and relatively horizontal femoral necks as seen in *Homo erectus* indicates well-developed ad- and abduction, which is obviously not an adaptation for running, but would not be unexpected and indeed would be advantageous for a species that had to regularly wade, tread water, swim or climb. In *Homo sapiens* the pelvis (bi-iliac diameter) did become narrower and the femoral necks shorter and more vertical, and we agree with Bramble and Lieberman that this could be related to more frequent terrestrial locomotion.

Plantar arches, enlarged tubera calcanei, close-packed calcaneo-cuboid joints and short toes are not seen in cursorials, whether bi- or quadruped, to the contrary: running species are typically unguli- or digiti-, not plantigrade and typically have elongated toes.

In conclusion, comparative data suggest that none of the features described by Bramble and Lieberman (2004) are typical either of savannah dwellers or frequently running animals, whether slow or fast. Until the features are considered in the context of swimming and wading as well as terrestrial movement, their interpretations should be considered with extreme caution. As it is, there is no obvious reason why any of the features cited could not have been of advantage in a littoral environment. We do not deny that humans today are adapted to terrestrial locomotion including walking and moderate running, but in our opinion the peculiar human anatomy is *not directly* derivable from a typical primate ancestor who moved from closed to more open, arid habitats.

At least two conspicuous anatomical features of *Homo erectus* are notably not included in the list of features cited by Bramble and Lieberman (2004).

1) *Homo erectus* typically has a more robust, and therefore heavier, skeleton than all other (fossil and extant) primates, including *H. sapiens* and the other apes. One of its defining characteristics is the shape and size of the femoral bone, which shows cortex thickening and densening (*pachyostosis*) and a narrow cavity of the bone marrow (*medullary stenosis*). The cranial bones, especially the posterior part (the occiput), are also notably thicker than in other primates including *H. sapiens*. Unusually heavy bones would be a disadvantage for a species relying on endurance running, and are not seen in running mammals such as dogs or horses, whereas for a species collecting

sessile food from the water's edge, including underwater foraging, they could have been a significant advantage. Human divers such as the Ama of Korea frequently use weights to help them descend (Hong and Rahn 1967). Slow-diving mammals for sessile foods typically have medullary stenosis and pachyostosis to a higher degree than in *H. erectus* (walruses, dugongs and fossil littoral species such as *Kolponomos*, *Odobenocetops* and some *Thalassocnus* species), while fast-diving mammals for mobile prey have light-weight bones (dolphins and sealions).

2) *H. erectus* had less basicranial flexion than *H. sapiens*, meaning that the eyes would have been more naturally oriented towards the sky if they were standing with an upright posture (remembering that we do not know for certain which posture *H. erectus* may have preferred when on dry land), rather than directed more towards the horizon, as is the case when *H. sapiens* stands with an upright posture. This would be a disadvantage for a species relying on endurance running because, among other things, more energy would be needed to look at where the feet were making contact with the ground. In a diving position, as well as in a more procumbent body position while wading for food, for example, the less flexed cranial base would have resulted in the eyes being more naturally oriented in the direction the individual was moving (i.e., in the case of swimming and diving, head first through the water). We are not aware of any models which suggest early *Homo* ran with a bent hip posture, but we do note that human sprinters generally run with the body leaning forward.

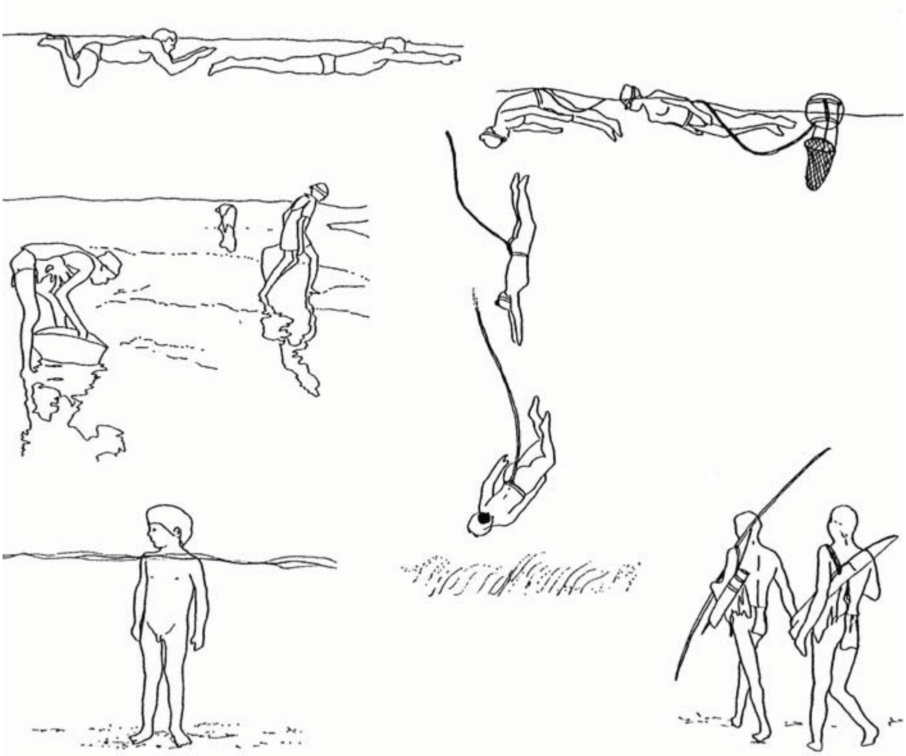

Figure 4. All available data suggest human locomotion *primarily* adapted to the waterside rather than to the open plains (from Bender *et al*. 1997).

Within many contemporary *H. sapiens* populations there are individuals who are capable of long distance running, but compared to typical savannah species, humans are slow and inefficient (Figure 4). Moreover, recent research suggests that endurance training in athletes sometimes causes cardial arrhythmias and sudden death (Ector *et al*. 2007). Even Bramble and Lieberman (2004) admit that "humans are mediocre runners in several respects" and "running is more costly for humans than for most other mammals". And since *H. erectus* generally had, for instance, heavier bones than *H sapiens* and longer femoral necks, it must have been an even less efficient cursorial than extant *H. sapiens*.

FOOD COLLECTION AND PROCESSING IN HUMAN ANCESTORS

Finding and being able to procure adequate amounts of food are obviously essential for the survival of any population. Humans are more omnivorous than other apes, suggesting a shift in diet since our linage separated from chimpanzees. Traditionally, anthropologists have speculated that large savannah mammals (either hunted or scavenged) played an important role in this shift, but we consider it more likely that the initial shift in diet occurred with smaller, sessile prey, such as invertebrates, which could have been easily procured by our ancestors, even before they had diverged from the ancestral lineage leading to chimpanzees. A diet increasingly reliant on waterside invertebrates such as shellfish could help explain the evolution of a large brain, and would be compatible with many other features characteristic of the *Homo* genus.

Acquiring Adequate Brain Nutrition

Cordain *et al*. (2000), in the tradition of the 'open plain' ideas, have suggested that the brains of large terrestrial mammals may have provided the *Homo* genus with the extra docosahexaenoic acid (DHA) needed to help fuel a large brain. While we fully agree that the structural, cognitive and visual development of the brain requires adequate amounts of certain nutrients including DHA (Crawford and Sinclair 1972), we think the initial shift might have included more abundant and easily obtainable DHA-rich sources such as shellfish, crayfish, fish, turtles, birds and eggs (Broadhurst *et al*. 1998), although we admit that this alone is insufficient proof for a waterside past (Carlson and Kingston 2007, but Cunnane *et al.* 2007).

Brains and vision evolved in the animal kingdom more than five hundred million years ago, whereby the principle building-blocks were aquatic fatty acids (Crawford *et al*. 1999). DHA (22C:6ω3) is a poly-unsaturated fatty acid that has a chain of twenty-two carbon atoms and six unsaturated bonds (on the carbon atoms in the positions C3, C6, C9, C12, C15 and C18 starting from the omega-end of the carbon chain). It is the only omega-3 molecule used by fish, amphibia, reptiles, birds and mammals for both visual and neural signalling systems. Since the primary source of DHA is algae and plankton, it is abundant in the marine and lacustrine food chains, but almost absent in the meat, fats and offal associated with carnivore remains (Broadhurst *et al*. 2002). This might partially explain why some marine mammals which eat high DHA level foods have large brains (e.g., 1.8 kg for dolphins), whereas it is hard to find a land mammal except humans and elephants with brains that weigh more than about 1 kg. The rhinoceroses which inhabit African savannahs weigh more than a thousand kilograms, but have brain weights of about 400 grams, three times less than humans.

Other brain-selective nutrients are also more abundant in aquatic than in terrestrial milieus. This is notably the case for brain-selective minerals such as iron, copper, zinc, selenium, and iodine (Table 5). Of all the major food groups, shellfish requires the least amount (900 grams) to meet the minimum requirement for all five minerals, and is also the food group for which these requirements are most evenly distributed. Eggs (2500 grams) and fish (3500 grams), both more abundant at the waterside than in terrestrial environments, are next, while 5000 grams of meat, five times more than shellfish, would be needed to meet the minimum daily requirements for all five minerals (Table 5). Iodine especially is more abundant in littoral food chains than terrestrial food chains, and before the iodinisation of drinking-water and salt, hypothyroidy caused by iodine deficiency resulted in mental retardation and cretinism in millions of humans who lived away from the coasts.

Rather than running over open plains to gain adequate nutrition, women, children and the elderly could have collected all the brain food they required without expending nearly as much energy, by inhabiting the water's edge. A littoral existence does not preclude the hunting, scavenging or butchering of land animals (which often gather, drown and get bogged at the water's edge), nor the gathering of anti-oxidant rich plants, fruits and tubers that grow in abundance in moist regions besides estuaries, rivers, lakes and deltas (Wrangham 2005).

Table 5. Daily amount of major food groups (in kilograms), arranged from low to high, minimally required for five brain-selective minerals: iodine, iron, copper, zinc and selenium (I, Fe, Cu, Zn and Se), after Cunnane (2005)

	I	Fe	Cu	Zn	Se
shellfish	.7	.8	*.9*	.5	.3
eggs	.2	.6	*2.5*	.9	.9
fish	.2	*3.5*	3.1	2.7	.7
pulses	*3.7*	.4	.3	.5	3.0
cereals	3.2	3.1	*4.8*	1.9	2.2
meat	1.5	.8	1.7	.9	*5.0*
nuts	1.5	.8	.9	.5	*5.5*
vegetables	4.2	2.1	2.7	*8.7*	6.7
fruit	6.0	3.7	4.8	*9.3*	6.0
milk	6.7	24.0	12.5	*47.0*	5.5

The figure in *italic* is the most limiting factor in each food group.

Some other Considerations regarding Food Acquisition

a. Tool Use

Tool use is easily explained in a model where human ancestors foraged at the water's edge, where removing and open hard-shelled foods such as nuts, fruits and shellfish, would have been rewarding. Chimpanzees, capuchin monkeys and different otter species are all known to use tools to open hard-shelled foods. The *Homo*/*Pan* ancestral population was most likely at least partly arboreal, and early *Homo* ancestors might have lived in flooded forests where they could have collected fruit from the trees, and molluscs attached to tree roots, branches and trunks, as capuchin monkeys do today (Fernandes 1991).

b. Dental and Masticatory Reduction

Compared to australopithecines (large cheekteeth) and apes (large canine teeth), *Homo* typically has reduced dentition, and several archaic fossils (*H. georgicus*, *H. erectus* and *H. neanderthalensis*) show extensive tooth loss and bone resorption of tooth alveoli in older individuals, or even congenital generalised enamel dysplasia (Fischman 2005, Zilberman *et al*. 2004). Such dentitional atrophy is incompatible with an, even partial, dependence on carcass consumption on open plains, but is less of a problem or might even have been advantageous in a shore-based lifestyle where consumption of slippery foods such as shellfish might have been important. In the same way, hunting or scavenging lifestyles fail to explain the drastic and apparently abrupt reduction of human masticatory musculature (Stedman *et al*. 2004). Humans not only lack the sharp dentition of dogs and hyenas, but also their strong biting and chewing muscles.

c. Olfactory Reduction

Savannah-based large mammal consumption is hardly compatible with the drastically reduced olfactory capacity of humans compared to apes (Gilad *et al*. 2003). Dogs and hyenas rely on their superb olfactory abilities to detect carcasses, whereas to collect and consume water-side shellfish a sense of smell is unimportant. Underwater foragers have small (Pinnipedia) or absent (Cetacea) olfactory lobes in the brain compared to terrestrial mammals (Macdonald 2001).

d. Very Sensitive and Mobile Hands

Primates have more sensitive and mobile hands than most other mammals, especially cursorial and savannah-dwelling ones, but this is even more so the case in humans. Comparable trends are seen in waterside mammals such as racoons (*Procyon* species), marsh mongooses (*Atilax paludinosus*), and Cape clawless otters (*Aonyx capensis*), which have unwebbed and highly sensitive and mobile fingers used to forage for crabs and shellfish at the waterside (hence the term ‘Fingerotter’ in German). Such trends are not seen in savannah-dwelling mammals.

e. Subcutaneous Fat

Humans have about ten times as much subcutaneous fat as most terrestrial mammals and non-human primates including chimpanzees, and in this respect they approach ‘lean’ aquatics such as fin whales (Pond 1987). Greater distribution of subcutaneous fat is seen in all endothermic species that spend a lot of time in water, and could have been an advantage for humans in a waterside context (whether for energy storage, thermo-insulation in water, hydrodynamic streamlining, buoyancy, or other ‘purposes’). On the other hand, extra fat would be a disadvantage for an animal reliant on endurance running, which is clear when fat levels of marathon runners are compared with those of long-distance swimmers, who typically are three to five times fatter than long-distance runners (discussion and references in Verhaegen 1991).

PALAEOECOLOGICAL EVIDENCE

Overall, there are many different lines of evidence that point to the evolution of *Homo* at the water's edge. The waterside model is based in the first place on comparative anatomical data such as subcutaneous fat and lack of fur (Westenhöfer 1942, Hardy 1960), but nutritional, and comparative behavioural data are also compatible. It is often assumed the real 'hard evidence' (bones and stones) points to a savannah existence for early *Homo* species such as *erectus* and *ergaster*. Our research, however, suggests the earliest *Homo* fossils and artefacts and those throughout the Pleistocene are consistently associated with habitats in which water was apparently plentiful, and where underwater foraging would have been both possible for human ancestors and rewarding.

Although the fauna associated with early *Homo* sites is often cited as evidence in support of the open, semi-arid view (Reed 1997), these data are at best ambiguous when the waterside model is also taken into account. Palaeoecological evidence associated with *Homo* fossil and archaeological sites strongly suggests that *Homo* may well have been a waterside dweller (Munro 2004).

Although, due to taphonomic considerations, caution is required when interpreting fossil and archaeological data, the results of our preliminary survey reveal that, from its earliest appearance, all *Homo* sites (i.e., fossil *Homo* sites as well as archaeological sites presumed to be *Homo*) are typically and consistently associated with waterside contexts.

Homo *Sites Older than 0.2 Ma* (Mega-anni, Million Years Ago)

At Gona, Ethiopia, 2.5 Ma-old stone tools were deposited in "floodplain environments, close to margins of channels that carried the volcanic cobbles used as raw materials for tool manufacture" (Semaw *et al.* 1997: 333). Nearby, in the Hata Member of the Bouri Formation, hominid fossils of a similar age to the Gona deposits were discovered in sediments containing sandstone with bivalve and gastropod shells "deposited by fluvial processes associated with floodplains along distributary channels close to a shallow fluctuating lake" (de Heinzelin *et al*. 1999: 625). This Member also reveals evidence of cut and percussion marks on bones of medium and large-sized bovids, though stone tools have so far not been discovered.

The *Homo* maxilla AL 666, dated to 2.3 Ma, along with a stone tool assemblage (though no signs of butchering), was recovered from deposits of the Hadar Formation, suggesting a landscape which was "predominantly open, with wetlands and bushed or wooded grasslands, and with stands of trees close to the water source" (Kimbel *et al*. 1996: 559).

At Olduvai Gorge, Plio-Pleistocene *Homo* remains are associated with deposits containing "cemented aggregates of the small benthic, freshwater clam *Corbicula*" as well as crocodiles, hippos and fish (Blumenschine *et al.* 2003: 1220). Cut and percussion marks are found on a percentage (4.2 and 8.3% respectively) of the long bones of larger mammals. Fish and gastropods, judging by the remains of 'living sites', might have been consumed at Olduvai Gorge, while the avian fauna included abundant waders (flamingoes, herons, storks, rails, jacanas, plovers, sandpipers and stilts), swimmers and divers (grebes, cormorants, pelicans and ducks) as well as marine birds (gulls, terns and skimmers) (Leakey 1979).

The earliest occurrence of the genus *Homo* in the Turkana Basin is associated with floodplain deposits in which gastropods, fish, crocodiles, bovids, equids, suids, cercopithecids and hippopotamids occur (Pratt *et al*. 2005). During Plio-Pleistocene times the Turkana Basin contained a large lake fringed by swampy wetlands as indicated by the numerous fossils of hippos, crocodiles, fish (including a stingray, suggesting a marine connection at the time), gastropods, bivalves, sponges and numerous ostracods. Lung fish, water bucks, cane rats, monkeys, giraffes, buffaloes, camels, rhinoceroses and elephants suggest a rich mosaic of wet, dry, open and closed habitats in the vicinity of an extensive lake, or large river (Feibel *et al*. 1991).

Table 6. Taxa found in Unit 2 at Nariokotome III (from Walker and Leakey 1993)

Taxa	Lifestyle and habitat
Pila ovata	Air-breathing, shallow-water swamp snail
Claria sp.	Shallow-water catfish
Clarotes sp.	Catfish
Hydrocynus sp.	Shallow- to deep-water fish predator
Synodontis sp.	Shallow-water spiny catfish
Varanus niloticus	Scavenging and often aquatic lizard
Trionyx sp.	Soft-shelled freshwater turtle
Pelomedusidae spp.	Smooth-shelled water tortoise
Homo erectus	Waterside hominid (this study)
Metridiochoerus sp.	Grazing pig
Hippopotamus aethiopicus	Aquatic herbivore
Hippopotamus gorgops	Aquatic herbivore
Bovidae spp. (duiker- to buffalo-sized)	Grazing and browsing herbivores
Lepus capensis	Grass and herb feeder

The most complete skeleton of an early *Homo* specimen, KNM-WT 15000, the so-called ‘Turkana Boy’ of Nariokotome, Kenya, was discovered on the western side of the Turkana Basin. It lay among reeds and hippopotamid footprints, and the most abundant faunal remains associated with it were water snails, fish and turtles (see Table 6).

The Plio-Pleistocene Shungara Formation in the Omo Basin contains an archaeological assemblage as well as molluscs (including freshwater oyster *Etheria* reefs), fish, crocodiles, hippopotamids, bovids, cercopithecids, turtles, suids and other vertebrates. The archaeological occurrences “are all in proximal river settings” (Clark Howell *et al.* 1987: 696).

In the Western Rift Valley, the Senga 5A site (2–2.3 Ma) contains artefacts associated with gastropods, bivalves, fish, hippopotamids, suids and bovids in a “low-energy littoral lacustrine setting” (Harris *et al*. 1987: 724).

The Plio-Pleistocene Chiwondo Beds of Malawi have yielded *Homo* fossils as well as fragmented remains of fish, turtles, crocodiles and large mammals. They also contain molluscs “in consolidated beds of carbonate cemented sandstone. Molluscan shell beds crop out as benches up to several meters thick and several hundred meters wide” (Schrenk *et al*. 1995: 59).

The late Pliocene Chemeron hominid (KNM-BC 1) was deposited in a lake filled basin where fish remains were abundant: “Molluscs also lived in the lake, and locally their remains accumulated to form shelly limestones. … There is little doubt that the fossil came from the Upper Fish Beds" (Martyn and Tobias 1967).

The Dmanisi *Homo* fossil site, dated to 1.8 Ma, is located at the confluence of two rivers, where at the time a lake or pond had formed due to the blocking of a river by a lava stream. "The hominid site itself was likely located near a lake or pond, rich in lacustrine resources. This biome, together with the adjacent forest-steppe formations, created a highly productive ecotone rich in animal and plant resources" (David Lordkipanidze, personal communication to MV). The inhabitants might have eaten hackberrys, since abundant seeds have been found at this site (Gabunia *et al*. 2000).

Early Pleistocene archaeological sites from the Jordan Valley include Erk-el-Ahmar and 'Ubeidiya. These sites are associated with lacustrine and fluvial deposits rich in fresh water gastropod and bivalve remains as well as fish, turtles, hippos and birds (Bar-Yosef and Tchernov 1972).

Aïn Hanech, an archaeological site in Algeria dated to about 1.8 Ma, was formed on an alluvial floodplain cut by a meandering river (an oxbow lake), and may indicate repeated activities by hominids at a shallow river embankment (Sahnouni *et al*. 2002).

At Pabbi Hills, Pakistan, artefacts of Pliocene age, about 2 Ma, have been discovered in deposits which also contain crocodiles, turtles, aquatic gastropods and bivalves. The molluscs suggest a large, slow-moving river with clean, shallow water less than five meters deep, analogous to unpolluted sections of the Ganges River (Dennell 2004).

The site of Mojokerto (Perning), on the Island of Java has been dated to between 1.5 and 1.8 Ma. This coastal deltaic environment (Huffman 2006) contained fresh water and marine molluscs, which would have been easily procured and consumed by early hominid inhabitants (Frank Wesselingh, personal communication to SM).

At Sangiran, also on Java, where *H. erectus* was found, "a thin layer of diatoms (unicellular marine phytoplankton) and dark clays with a marine musselfauna was deposited by the sea, as was noticed and described before by Professor Martin from Leiden" (von Koenigswald 1981).

Hominids on Java were using mollusc shells to butcher mammals, presumably to gain access to nutritious meats, as early as 1.5 Ma (Choi and Driwantoro 2007).

The archaeological site of Majuangou (Nihewan), in China, recently dated to 1.66 Ma, reveals that hominids inhabited a lake filled basin, where the remains of aquatic molluscs, and the leaves and fruits of aquatic plants have been discovered, indicating a low energy lakeshore or marsh environment (Zhu *et al*. 2004).

In the Middle Awash of Ethiopia, the Daka Member of the Bouri Formation, dated to 1 Ma, contains artefacts, *Homo erectus* cranial and post cranial bones, abundant hippo fossils, as well as gastropods and bivalves associated with alluvial, lakeside beaches or shallow water deposits in distributary channels (Asfaw *et al*. 2002).

Buia, in Ethiopia, contains *Homo erectus* fossils and artefacts dated to 1 Ma. These occur in deltaic deposits of the Alat Formation, which also contains fish and freshwater gastropod (*Melanoides*) remains (Abbate *et al*. 2004). Evidence that hominids butchered medium to large-sized bovids, hippos, and a crocodile, also come from these deposits (Fiore *et al*. 2004).

A partial *Homo* cranium from the same stratigraphic level as Acheulian artefacts from Olorgesailie, Kenya, has been dated to between 0.97 and 0.9 Ma. The sandy silt adhered to the frontal bone of this specimen contained amphibian bones and the tooth of the swamp rat

Otomys sp., which today inhabits thick grasses in and around the swamps, lakes and rivers of East Africa (Potts *et al*. 2004).

The Angolan site of Dungo V reveals evidence for the exploitation of a large whale (*Balaenoptera sp*.) on a former beach possibly more than 1 Ma. Closely associated with the whale skeleton were numerous Lower Palaeolithic artefacts, together with numerous molluscs, other marine invertebrates and shark teeth (Gutierrez *et al*. 2001).

The earliest evidence for human activity in northern Europe comes from the site of Pakefield, England, about 0.7 Ma, where artefacts from estuarine silts containing marine fauna have been discovered. The majority of artefacts derive from '*Unio* bed' coastal river deposits (Parfitt *et al*. 2005).

Homo *Sites from 200 ka to 50 ka* (kilo-anni, Thousand Years Ago)

The earliest evidence for *H. sapiens* in the fossil record comes from the Ethiopian Kibish Formation in deposits dated to 195 ka. This formation consists of "flat-lying, tectonically undisturbed, unconsolidated sediments deposited mainly in deltaic environments over brief periods" (McDougal *et al*. 2005: 733). Human remains derive from essentially the same archeological level that remains of the fresh water oyster *Etheria* have been found.

Also in Ethiopia, *H. sapiens* and stone artefacts occur in the Herto Member of the Bouri Formation at 160 ka. This member contains gastropods, bivalves and (often butchered) hippopotamus bones, testifying to a waterside setting (Clark *et al*. 2003).

In Eritrea, the 125-ka-old Abdur Archaeological Site, on exposed Red Sea reefs, indicates that humans were using tools to "harvest shallow marine food resources and possibly to butcher large land mammals on the ancient shoreline" (Bruggemann *et al*. 2004: 180).

On the Mediterranean coast of Africa, the Haua Fteah site reveals evidence that *H. sapiens* were harvesting and consuming shellfish 80–100 ka (McBurney 1967), while at the coastal sites of Gibraltar (Barton *et al*. 1999) and Liguria (Stiner 1994) there is evidence that *H. neanderthalensis* was collecting and consuming shellfish.

Along the African Cape coasts there are many Middle Stone Age (MSA) sites with abundant shellfish and other marine food remains. The total number of sites may be in the hundreds. These sites are associated with some of the earliest modern human remains (see review in Broadhurst *et al*. 2002). The best known is Klasies River Mouth, where 20 meter deep shell middens occur, mostly dating to Oxygen Isotope Stage 5 (Grun *et al*. 1990, Deacon 1992). These deposits show "evidence for the exploitation of marine resources" (Thackeray 1988: 27). The shell middens associated with Blombos Cave, dated to 80–100 ka, indicate that marine molluscs were the "most abundant category of food waste" (Henshilwood *et al*. 2001: 441) and at Die Kelders the cave deposits contain "bones of seals, dolphins and marine birds" (Grine *et al*. 1991: 375).

On the Atlantic coast, the sites of Sea Harvest, Hoedjies Punt and Ysterfontein reveal evidence that the inhabitants were harvesting marine limpets and mussels (Volman 1978, Klein *et al*. 2004). Many more west coast MSA shell middens are known, but are as yet unexcavated.

The adipose tissue and organs of seals and sea birds, and the egg yolks of sea birds and turtles, which consume exclusively marine/littoral foods, are rich in DHA (Broadhurst *et al*. 1998, Speake *et al*. 1999). Cape penguins could have been scavenged or even hunted fairly easily, especially the eggs and nestlings. Collecting fresh eggs and live flightless nestling birds in a littoral environment could therefore have potentially provided the greatest amount of LC-PUFA (long-chain poly-unsaturated fatty acids) for the least amount of effort of any terrestrial food source known (Broadhurst *et al*. 2002).

Evidence from the Willandra Lakes in Australia confirms that at least by 50–46 ka (Bowler *et al*. 2003) and possibly as early as 63 ka (Thorne *et al*. 1999, but see also Bowler and Magee 2000, Gillespie and Roberts 2000, and Grun *et al*. 2000), humans were creating shell middens dominated by the fresh water mussel *Velesunio*, and hearths containing remains of the golden perch *Plectroplites* (Bowler *et al*. 1970). The earliest evidence of human occupation from New Guinea comes from uplifted coral reef terraces on the Huon Peninsula, which reveal some of the earliest (possibly 45–53 ka) examples of hafted axes known anywhere in the world (Groube *et al*. 1986).

Significantly, coastal fossil and archaeological sites older than about 125 ka are extremely rare because most coastal caves are younger than 125 ka, or have been flushed of older deposits by wave action or other erosion (Klein *et al*. 2004). Sea levels for much of the Pleistocene were lower than today, so the vast majority of Pleistocene coasts are now under water. Despite this, a number of *Homo* fossil sites older than 125 ka are known, such as the 1.5- or 1.8-Ma-old Indonesian site of Mojokerto, the whale butchering site of Angola, and the 700-ka-old Pakefield site from England. The non-coastal sites are generally associated with permanent water bodies such as rivers and lakes, that in most cases appear to have been connected, at least for a time, with the coast, for instance Turkana, Dmanisi, Nihewan, Erq el-Ahmar, Aïn Hanech, and Pabbi Hills.

H. sapiens appears to have a strong correlation with shellfish, starting with its earliest appearance in the fossil record, and continuing throughout the Pleistocene and Holocene to modern times. Huge shell middens and evidence of aquatic exploitation are known from coasts, rivers and lakeside settings all over the world from recent times well back into the Pleistocene (see Fairbridge 1976, Meehan 1982, Shackleton and van Andel 1986, Waselkov 1987, Erlandson 2001).

The data presented here are far from complete (archaic *H. sapiens* fossil sites from China, for example, are not included) and we acknowledge that a more detailed survey is necessary to provide a clearer picture. Yet, as far as we know, this is not an unrepresentative sketch of what is currently known about early fossil and archaeological *Homo* sites, and *H. sapiens* sites in particular from Africa prior to the last glacial. Even if there is a clear association between *Homo* remains, however, and permanent water and shellfish, this can not in itself be seen as proof that *Homo* was a water-side dweller. Other lines of evidence are important.

DISCUSSION

Several palaeontologists, adverse to the idea that part of our evolutionary history may be linked to an aquatic environment, claim that it is not parsimonious to go from land to water, and then back to land, in order to explain how we evolved running abilities.

First it should be noted that Bramble and Lieberman’s (2004) idea that endurance running was a “major contributing factor” to the evolution of the human body form is not based on comparative biological evidence and is unclear in terms of the motivation and timing of key events. For example, nowhere is it detailed whether endurance running developed before or after large brains, and how these events relate to the need to obtain extra fats and proteins. It seems also unclear which *Homo* species may have been endurance runners. Despite the lack of these crucial details, the ‘endurance running’ model forms the basis for further research. For example, Arcadi (2006) compares wolf-like canids to Pleistocene hominids because he assumes they are “behaviourally similar” and that both are “adapted for endurance running.”

In our opinion, the ‘water’s edge’ hypothesis is backed by robust data, and is a more parsimonious model than ‘open plain’ models including the traditional savannah and ‘endurance running’ models. The waterside hypothesis is consistent with behavioural, comparative and nutritional data, as well as with evolutionary theory (natural selection, gradualism, mosaic evolution, parallelisms and convergences, and sequences of overlapping functions and niches). It helps explain typically human features that are rarely seen in open terrain cursorial mammals, such as tool use, breath-hold capacities, diving skills, nakedness and external nose.

Moreover, it provides an evolutionarily plausible explanation for our lineage’s transition from arborealism to terrestrial bipedalism. Whereas comparative evidence suggests that a *direct* transition from the trees to the plains would induce a more quadrupedal form of locomotion (as seen in savannah baboons), an intermediary phase of vertical wading and climbing could plausibly explain a gradual evolution towards present-day human bipedalism (Stringer 2001, Kuliukas 2002). Other water-based scenarios, based on swimming and underwater foraging, are also conceivable, and are easily derived from climbing–wading lifestyles (Verhaegen *et al.* 2002). Although hypothetical, the wading–climbing scenario for bipedalism is not a ‘just-so’ construction of the kind that is used in ‘open plain’ arguments (Table 2), because there is comparative evidence of bipedal wading in arboreal species such as mangrove-dwelling proboscis monkeys (Figure 5) and in lowland gorillas dwelling in forest swamps (Doran and McNeilage 1997).

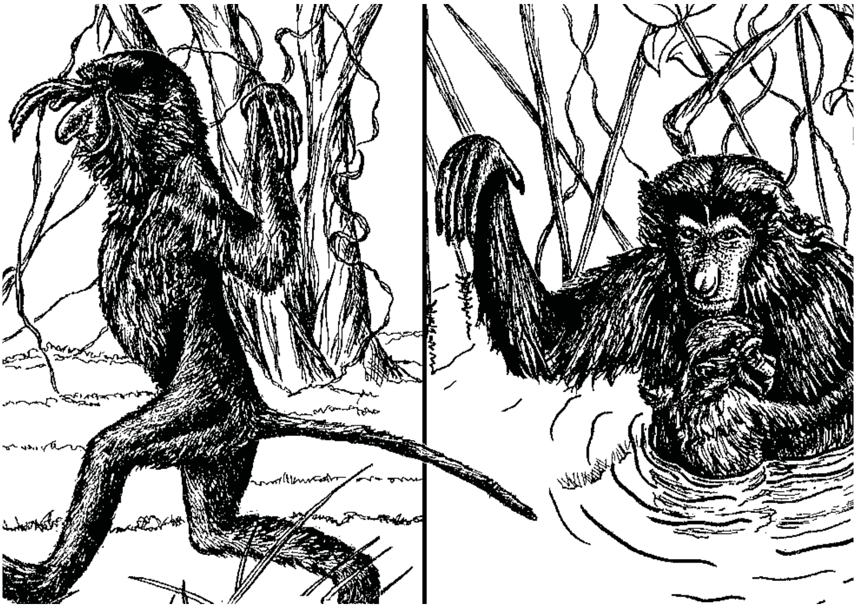

Figure 5. Proboscis monkeys (*Nasalis larvatus*) walking bipedally on land and wading bipedally in mangrove swamp (after an illustration of Amanda Williams in Morgan 1997: 65). “While wading, the

monkey uses an upright posture, with the females carrying infants on their hip. Troops have been filmed continuing to walk upright, in single file, along forest trails when they emerge on land, the only non-human mammal, with the exception of gibbons and giant pangolins, known to use this form of locomotion for any length of time." http://en.wikipedia.org/wiki/Proboscis_Monkey

Human waterside ancestors might have searched for and gathered foods from the shallow waters of flooded coastal, riverine, lacustrine, deltaic and swamp forests (Sauer 1962, Roede *et al*. 1992, Verhaegen *et al*. 2002, Wrangham 2005). They could have learnt to dip their heads under water to search for food, and could have gradually become more efficient swimmers and mobile underwater foragers (Hardy 1960, Morgan 1997, Vaneechoutte 2000).

In this scenario, ancestral human populations could have been increasingly capable of exploiting an increased range of foods from the shore and from under the water, becoming more omnivorous as they increasingly gained access to a rich source of easily obtainable nutritious foods such as insects, coconuts, shellfish, crabs, fish, frogs, eggs, as well as terrestrial, arboreal, aquatic, large and small reptiles, birds and mammals. Occasional or regular consumption of stranded whales (Gutierrez *et al*. 2001) or drowned or trampled bovids crossing major rivers could account for the instances where butchering of carcasses with shell (Choi and Driwantoro 2007) or stone tools have been described archaeologically.

In order to forage more efficiently underwater, a more alined body (with head, spine and legs all in one line) would have been an advantage, while relatively long legs could have been useful for wading, treading water, swimming, diving, terrestrial bipedalism and climbing, particularly palm trees. Present-day human running can therefore be parsimoniously derived from an ancestral body shape designed to perform a number of different activities at the water's edge, not just at the forest–savannah interface.

And it should be emphasized again that, in order to acquire the minimum daily requirements for humans including brain-specific poly-unsaturated fatty acids, the resources associated with littoral habitats are much more easily accessible to primates than the brains of large mammals, which have to be removed from the skulls of dead animals and for which there is a fierce competition with large mammalian predators and scavengers, who are far better equipped for finding carcasses, cracking skulls and predation.

CONCLUSION

The 'endurance running' hypothesis of Bramble and Lieberman (2004) appears to have been accepted without discussion by many members of the scientific community and has largely remained unchallenged. It is one of the latest examples of the 'open plain' way of thinking, which can be traced back to the beginning of the 19th century. After the discovery of the first African fossil hominid by Raymond Dart (1925), this model was considered to be supported by hard evidence. This first australopithecine fossil was found in a region that is now a marginal desert habitat, but which was a much wetter habitat at the time of preservation. We have presented data showing that 'open plain' models are inconsistent with Darwin's theory that adaptation and analogies (convergences and parallelisms) as well as continuity and gradual functional shifts (*Natura non facit saltum*) are essential factors in evolutionary processes (e.g., Darwin 1903: 171, 82). There are a number of lines of evidence, including behavioural, biological, anatomical and nutritional data, inconsistent with ‘open plain’ models.

These same lines of evidence, on the other hand, fit remarkably well with the ‘waterside’ model. This model is consistent with all the available archaeological and fossil data. It explains much more satisfactorily the transition from tree-climbing to vertical terrestrial bipedalism, and helps explain otherwise unexpected traits such as our large brain, tool use, breath-hold diving abilities, protruding nose, alined body, subcutaneous fat deposits as well as other characteristics. These traits are often shared with waterside and aquatic mammals, but are not seen in plains- or savannah-dwelling mammals. The waterside model does not preclude the hunting, scavenging or butchering of large mammals, nor terrestrial bipedalism, but renders unnecessary endurance running over open, semi-arid plains.

Considering all we now know, the waterside model is the most parsimonious explanation for the evolution of many of the typical features in which the genus *Homo* differs from other primates. We predict that a more detailed and systematic study of the human features involved in locomotion, combined with an acceptance that wading, swimming and underwater foraging may have been important locomotor activities, will lead to a better understanding of our evolutionary past.

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Chapter 7

SOIL ENGINEERS AS ECOSYSTEM HETEROGENEITY DRIVERS

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ABSTRACT

Ecosystem engineers function as regulators of ecosystem functions by influencing the fluxes of energy and materials across different spatial and temporal scales. Understanding how ecosystem engineers affect the dynamic of heterogeneity in ecosystems is becoming a fundamental component of both theoretical and applied Ecology. This manuscript offers a conceptual discussion for characterizing how and why soil engineers (earthworms, termites and ants) affect heterogeneity patterns.

There are two types of ecosystem engineers in soils. Extended phenotype engineers concentrate their activities on the building of biogenic structures (earthworm casts, galleries and nest structures) in order to maintain optimal conditions for their growth. Conversely, accidental engineers expend energy in moving through the soil to find their optimal environment. Although both types of engineers create patches in an ecosystem, we argue that extended phenotype engineers have more effects on ecosystem heterogeneity since their activities are more concentrated in space, as compared to accidental engineers, which move and contribute to homogenisation of ecological processes throughout the whole ecosystem. Finally, we discuss how soil engineers affect ecosystem processes (e.g., carbon, water, and nutrient cycling) at higher scales than those of their own functional domains. While some biogenic structures can be looked on as

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patches or hot-spots without any interactions with their neighbourhoods at small space scales, others interact and constitute gradients and networks that significantly affect ecosystem processes, such as the population dynamic of trees or soil erosion at the landscape scale.

We argue that it is necessary to have a quantitative knowledge on the size, boundaries and dynamics of patches created by soil engineers. Embracing the links between the ecology of engineers and the frontiers of their sphere of influence will enhance understanding how spatial heterogeneity regulated by ecosystem engineers affect pools and fluxes in ecosystems.

INTRODUCTION

Many ecosystem goods and services such as water quality, top-soil organic matter content, and plant biomass production can be considered as cumulative outcomes of ecological processes that are inherently variable in time and space (Lovett et al., 2005). This heterogeneity of ecological systems has important functional consequences, for example in affecting plant growth and diversity (Tongway & Ludwig, 2005), soil carbon storage (Turetsky et al., 2005) or even hydrology (Steinman & Denning, 2005). The patterns of ecological processes can be described as patchworks, gradients and networks. Patchworks refer to a situation in which a property changes abruptly at boundaries that enclose patches that are themselves relatively homogeneous. Consequently, patches can be looked on as discrete or non-continuous units of area with delimited boundaries. Conversely, gradients are continuous variations (i.e., without boundaries) of a variable, and networks are connected, hierarchically branching elements of structure and function among patches (White & Brown, 2005). Although frequently considered as important, spatial heterogeneity in ecosystems is poorly quantified and understanding how these heterogeneities affect ecosystem processes is becoming one of the key needs for scaling up to global studies and for proposing sustainable land-use managements.

Heterogeneity patterns are driven by abiotic and biotic factors that are heterogeneously distributed. They are the product of history, and interaction between geology, topography, climate, vegetation and animals that create and maintain physico-chemical and biological heterogeneity over the full spectrum of time and space. At broad spatial and temporal scales, abiotic factors (climate and geology) set the stage of heterogeneity and determine physical properties, biochemistry, and biotic assemblages (Lovett et al., 2005). At a smaller scale, ecosystem processes are controlled by the interactions between biotic assemblages (including human activities) and abiotic properties (Amundson & Jenny, 1997). Amongst biotic vectors of heterogeneity, *ecosystem engineers* were identified to play prominent roles. Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to the species, by causing physical state changes in biotic or abiotic materials (Jones et al., 1994, 1997). These organisms are especially important in soils where they control ecological processes and ecosystem services.

Crucial to life on earth, soils are a primordial compartment of terrestrial ecosystems. From ozone depletion and atmospheric CO_2 releases to biodiversity loss and water pollution, the global ecosystem is impacted in far-reaching ways by the processes carried out in the soil (Brady & Weil, 1999). To a great degree, soil quality determines the nature of the vegetation and the capacity of land to support animal life and society. The soil abiotic-forming factors (i.e., climate, geology…) are central to understanding the variability in soils at the landscape level and at the level of individual soil profile. Soil functioning, however, is mainly controlled at a smaller scale by biotic factors (i.e., vegetation, micro- to macro-fauna and microbes) (Bardgett, 2005). In soil, the relative importance of regulation imposed by ecosystem engineering has been assumed to be greater than regulation by trophic relationships because of the specific physical and chemical constraints observed in this environment when compared to above-ground conditions (Lavelle & Spain, 2001). Earthworms, termites, ants and plant roots have been identified as the most important soil engineers (Lavelle et al., 1997; Jouquet et al., 2006). They play significant and prominent roles in heterogeneity patterns in ecosystems, mostly by displacing soil organic and mineral compounds from some sites to others, and by producing biogenic structures, i.e. organo-mineral aggregates (faeces, mounds, aggregates and gallery walls) and macropores (galleries, chambers), with specific physical, chemical and biological properties. These structures are usually considered by soil ecologists as resource and activity hotspots, patches or even islands in the whole ecosystem where different rates or nature of ecological processes than the bulk soil occur. In such physical structures the diversity and quantity of litter transformers, micropredators and microorganisms are often different from those in the surrounding soil. Soil processes such as SOM mineralization and nutrient release can be either enhanced or slowed down depending on the age and composition of the biogenic structure (Lavelle et al., 1992; Brown et al, 2000; Lavelle et al., 1997; Jouquet et al., 2006). Different descriptive studies also showed that these “hot-spots” or “fertile patches” are much more favourable for plant growth than in the sharply differentiated “interpatch” areas, which are relatively impoverished. As a consequence, plant biomass and community structures are usually different near or on these structures as compared to the surrounding environment (Jolivet, 1996; Blomqvist et al., 2000; Jouquet et al., 2004).

The purpose of this chapter is to offer an innovative and straightforward framework about, and analysing the effects of soil engineers on the dynamic of heterogeneity in ecosystems.

LINKING ENGINEERING STRATEGIES IN SOIL AND ECOSYSTEM HETEROGENEITY PATTERN

A thorough understanding of why organisms can be regarded as soil engineers requires studying how the modifications they create can influence their biology through feedback effects. In soil, soil invertebrates have to face common (i.e. competition and predation) and specific constraints as compared to above-ground organisms: (i) Soil is a relatively poor quality feeding resource, (ii) soil has occasionally adverse moisture and temperature conditions, (iii) and soil physical properties such as porosity and density can make foraging difficult (Lavelle and Spain, 2001). As a consequence, soil engineers have evolved different strategies to optimise their survival and growth in soil.

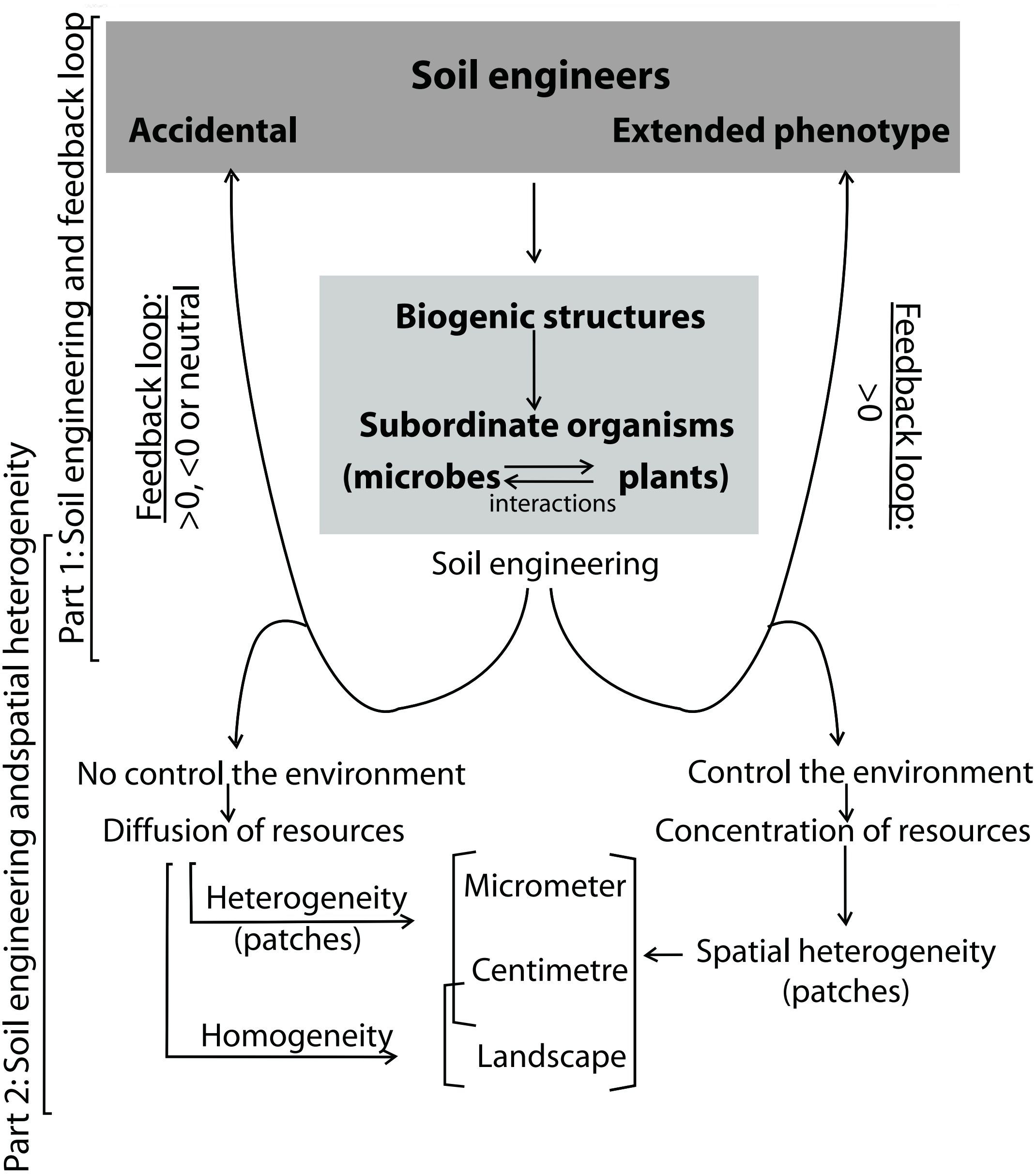

Figure 1.

Part 1. Effects of soil engineers on ecosystem functioning are mediated through the biogenic structures (nest, galleries...) and their respective effects on subordinate organisms (from microbes to plants). Extended phenotype engineers are organisms creating biogenic structures that are necessary for ensuring the engineer’s fitness while accidental engineers create structures that might have not essential positive, negative or neutral effects on themselves.

Part 2. Spatial movement in soil of accidental engineers contributes to the dynamic of heterogeneity at a low size scale, i.e. from micrometers to centimeters, and with a low intensity, but to the homogenisation of the soil physical and chemical properties in the whole ecosystem. The concentration or resources in hotspots by extended phenotype engineers leads to the creation of patches at both small and high spatial scales (from micrometer to the landscape scale).

Jones et al. (1994, 1997) defined the ‘extended phenotype engineers’ to refer to Dawkin’s work (1982), as organisms creating habitats or effects that directly influence their fitness. Conversely, engineers creating physical habitats that have no direct positive effect on themselves are called ‘accidental engineers’. The distinction between extended phenotype and accidental engineers is rather difficult, especially because it is difficult to assess whether there are correlations between the properties of habitats and the fitness of the organisms (Figure 1, part 1). This is especially true in soil where it is often difficult to determine how biogenic structures affect the survival and fitness of individuals, or colonies in the case of social insects. Soil engineering activities of termites and ants mainly consists in the construction of nest structures for the development of their colonies, and galleries and sheetings for foraging below- and above-ground. It is generally assumed that soil properties and architecture of nest structures allow termites and ants to decrease environmental hazards (i.e., predation, temperature and moisture homeostasis) and to optimize the development of the colony (Turner, 2000; Odling-Smee et al., 2003; Jouquet et al., 2006). The case of earthworms is a little bit more complicated. Earthworms can create either permanent or ephemeral burrows according to their feeding preferences (Lee & Foster, 1991; Bastardie et al., 2005). Two groups of earthworms can be differentiated: epi-anecic (feeding on soil and litter) and endogeic (feeding exclusively on soil). Epi-anecic earthworms are partially able to control their environment by living in more or less permanent burrows. These structures are formed as shelters from unfavourable environmental conditions, such as dryness or high temperatures. There structures have also been considered as a part of ‘external rumens’ that increase the palatability of SOM, which is then reingested by earthworms (Bouché et al., 1983; Brown et al., 2000). The survival and growth of earthworm individuals, and then probably also their fitness, are likely to depend on how efficient the properties of their casts and burrows are. Conversely, endogeic earthworm species move through the soil in order to find their thermal, moisture and feeding optima. As a consequence, these soil engineers are considered as more accidental engineers, since their biogenic structures do not seems to directly influence their fitness, than epi-anecic species. However, endogeic earthworms are never alone in soil and complex feeding interactions are likely to occur between individuals. How casting and burrowing activity affect endogeic earthworm populations remains unknown and requires further investigations. Most of the soil is affected by earthworm engineering activity and we can assume that endogeic earthworms, even if they do not feed on their own biogenic structures, are likely to consume the biogenic structures that have been made by other endogeic earthworm individuals.

One important difference between both types of engineers is the amplitude of their influence on soil spatial heterogeneity (Figure 1, part 2). Soil engineers affect soil processes and heterogeneity at widely different scales, ranging from soil aggregates and SOM dynamics to vegetation patterns and landscapes. However, the lifespan and size of their sphere of influence greatly depends on the functional groups and species considered. The sphere or influence of accidental engineers (i.e., most of the earthworm species) encompasses extensive spatial areas due to the burrows and macroaggregates they create through their movement for foraging in soil. Thus, random spatial motion contribute to the dynamic of heterogeneity at a low size scale, i.e. from micrometers to centimetres, and with a low intensity, but to the homogenisation of the soil physical and chemical properties in the whole ecosystem (Kretzchmar, 1989; Jouquet et al., 2006). In contrast, extended phenotype engineers have sphere of influence, which are more limited in spatial extent by creating more permanent structures such as nests of ants and termites. Although there is a gradient from accidental to extended phenotype engineers, we can assume that these two strategies differently affect ecological processes such as nutrient fluxes or vegetation growth and diversity. These effects of soil engineers on heterogeneity pattern in soils can also be initiated, or modified by, environmental heterogeneities (variation in temperature, moisture, availability of food…). One can also suggest that soil engineers can also reduce heterogeneity created by other biotic or abiotic factors. For example, the lifespan of microclimatic environments created by a piece of dead wood or a leaf fallen on soil will be reduced by the action of decomposer engineers (termites or earthworms). In these cases, ecosystem engineering activity will reduce the heterogeneity pattern in the ecosystem in response to their environments, or at least change it from one state (dead wood) to another (mixing of soil in the former site of the wood). Thus, feedback loops exist between soil engineers and environmental heterogeneities.

The above discussion emphasizes that it should often be possible to understand precisely and afterwards to predict the nature and magnitude of heterogeneity due to the activity of ecosystem engineers. For this, it will be useful to address at what scale do heterogeneities created by engineers become important (i.e., when can not be ignored). The answer will be that this scale depends on the question of interest, the type of heterogeneity affected, and the inherent scale of the units and processes.

BORDERS AND SCALE OF SOIL ENGINEERING

Although there is no doubt that soil engineering leads to the creation and maintenance of heterogeneity in ecosystem processes, how heterogeneity patterns affect ecosystem functioning at the scale of the landscape or watershed levels have rarely been studied. The sphere of influence of soil engineers (i.e., drilosphere, termitosphere, myrmecosphere and rhizosphere, *sensu* Lavelle et al., 1992) is usually considered through the biogenic structures themselves or the few cm around them. However, different studies showed that gradients and fluxes of energy and matter are possible and that the sphere of influence of engineering activity in soil can be of greater size than the physical frontiers of their constructions (casts, mounds...).

In this part, we will raise questions such as: what are the sizes of the sphere of influences of soil engineers? Are biogenic structures point processes, where rates are measured at a particular location, or do they lead to lateral transfers, where materials, energy, or information flow from one location to another? Are heterogeneity created by soil engineers statistics or dynamics?

Limit and Size of Biogenic Structures Produced by Extended Phenotypes

The concentration of activity of extended phenotype engineers promotes the maintenance of patches or islands that create a spatial and temporal mosaic of ecological processes. In the biomes where they are abundant, ants and termites can create long-lasting nests of prominent sizes. These nest-structures can be >2-6m in height, at densities between 200 and 1000 mounds ha^{-1} (Bardgett, 2005). Through their influence on nutrient cycling and water redistribution, they contribute greatly to the creation of the patch mosaics that characterize the soils and vegetation of many landscapes. These patches are usually considered to be point process or discrete units (*sensu* Lovett et al., 2005), or in other words to have delimited frontiers that impede intra-patches fluxes to spread to the surrounding environment. Indeed, there are plenty of examples in the literature showing that these patches have well definite frontiers with specific soil properties and vegetation communities (Dauber & Wolters, 2000; Dauber et al., 2001; Konaté et al., 1999; Jouquet et al., 2004) that make easily separate them from the surrounding environment.

However, there are also some evidences that these physical structures can interact with the surrounding environment through lateral flows (either gradient or network processes). Biogenic nests can serve as foci for nutrient redistribution in some landscapes and lateral flows have been shown to occur from these islands to the surrounding environments. For example, erosion of the above-ground termite nests leads to the accumulation of nutrients around the nests. As a consequence, the growth of plants is usually enhanced around termite nests (Spain & McIvor, 1988). Another example is the creation of vegetation-free zones around the nests of harvester ants (*Pogonomyrmex* spp.). Ants create and maintain these areas by removing debris and clipping the vegetation in order to reduce transit time for foragers, to decrease risk of exposure to fire and predation, and to increase exposure to solar radiation (MacMahon et al., 2000). Some studies also showed that nutrient leakages from the biogenic structures can occur and contribute to the regulation of trees in the overall system. In the Lamto savanna ecosystem (Côte d'Ivoire) termite-mounds are responsible for the spatial pattern of a common savanna palm-tree (*Borassus aethiopum*). It was shown that adult palm trees are able to exploit the mineral nutrients contained in termite mounds at log distances (at least 20 m) (Mordelet et al., 1996). This suggests that the palm tree is nutrient limited and that termite mounds influence its demography. All the palm tree stages are spatially associated with termite mounds but young stages grow on the average closer from mounds than adult stages (Barot et al., 1999) probably because young palms do not have a fully developed root system and cannot reach mounds a long distances. In addition, it was checked that seedling do have a higher survival rate when they growth at short distances from the mounds (Barot & Gignoux, 2003). Consequently, a biogenic island in an ecosystem that looks to function completely independently to the remaining system (Jouquet et al., 2004) can in fact be related to the overall ecosystem and play a significant role in the distribution of palm trees. Although it is difficult to estimate the time needed to produce these complexes interactions, we can estimate that biogenic structures have to last in a specific location for a long time. In this case, only extended phenotype engineers that produce and maintain long-lasting structures are concerned.

Distribution of, and interactions between nest-structures of social insects suggest that network processes can also occur through "meta-biogenic structures". This has especially been evidenced with ant species that produce polycalic nests (Booma et al., 1990; Chapuisat et al., 1997) and subterranean fungus-growing termite species (Josens, 1972) that produce interconnected nest structures from which diffuse mater, energy and information (i.e., ant and termite workers that share informations and food through trophallaxy). The role of these redistribution processes of energy and matter at the ecosystem scale has hardly been investigated. Although it is difficult to estimate the effect of these continuous fluxes on ecosystem functioning, we can assess that the mobilisation of resources, their transport and deposition in other nest units might be of great importance in the control of ecosystem functions. This effect of soil engineering on landscape heterogeneity pattern can either be positive (increase of heterogeneity through redistribution of energy along the whole ecosystem), negative (homogeneization of the properties at the ecosystem scale) or neutral (no significant effect on the existing heterogenity pattern).

These examples show that leaks of energy (e.g., nutrients from the biogenic structures) or ecological processes (e.g., clipping of the vegetation) from the biogenic patches to the surrounding environments can occur. Therefore, this underlines that the sphere of influence of ecosystem engineers can sometimes be higher than the physical frontier of the biogenic structures (nest-structures in these examples). These examples also show that ecosystems should not be considered as mosaics with “patches” that have independent ecological processes than those occurring in inter-patch environments. Biogenic structures must be defined on the basis of substrates and flowpaths that are absorbed from and dispersed to the whole ecosystem.

Large Scale Effects of Accidental Engineering

Soil accidental engineers are considered to contribute to heterogeneity pattern at small size scale, i.e. from micrometers to centimetres, and to homogeneise soil properties at the scale of ecosystem (Jouquet et al., 2006). Strayer (2005) considered that heterogeneity can be safety ignored if its grain size is much smaller than the spatial extent of the study area. Following this point of view and considering biogenic structures of accidental engineers as short-lived patches, requires to neglect their effects on ecosystem functioning. As a consequence, the effects of accidental engineers on heterogenity pattern are often neglected and ecologists, pedologists and agronomists do not include them in their studies and models of ecosystem functioning.

Since most of earthworm species do not maintain their casts and galleries and move through the soil, their biogenic structures are usually considered to be without any significant functional effect at the ecosystem scale (Lavelle & Spain, 2001). However, studies in a steep-slope ecosystem in the northern Vietnam showed that casts deposited on the soil surface and galleries made in soil by an epi-anecic earthworm species (*Metaphire leucorcica*) can persist for a long time, probably many years, owing to their great soil structural stability. Their exceptional resistance against disturbance is explained by the high clay and oxide contents in soils (Jouquet pers. com.). In the field, infiltration is locally increased due to cast roughness and preferential flow paths within galleries. Although biogenic casts and galleries are temporary structures for earthworms (in opposition to perennial nests of ants and termites), these structures do not disappear owing to their great soil structural stabilities and involve the permanence of the ecological processes (higher infiltration of water, decrease of the velocity of runoff water, decrease of soil detachability...) even if soil engineers do not maintain them. As a consequence, soil erosion is decreased at the scale of the study field (hectare scale) and, even if it has not been investigated, probably also contribute to the decrease of soil erosion at the watershed level. This example therefore shows that under specific conditions, accidental engineers can also promote heterogeneity that affects the whole ecosystem functioning (erosion in a watershed in our example).

Through their feeding and foraging strategies, accidental soil engineers can also influence plants at a broader scale than their biogenic structures by affecting SOM and nutrient cycling, seed transport and germination. The vast majority of studies on the effects of soil macrofauna on plants conclude that they can increase the growth of single plants but that the amplitude of this beneficial effect is species-specific (see Brown et al., 2000 for a review). Many hypotheses are proposed to explain this beneficial effect of earthworms on plant growth, including an increase of the availability of mineral nutrients in biogenic structures, a negative effect on pests such as nematodes, and so forth (Edwards, 2004; Blouin et al., 2005). While it has been recognized for some time that earthworms can have differential effects on plant functional groups, the consequences of this for vegetation at the landscape scale have hardly been investigated. The studies that have been done have looked at effects of earthworms on grassland plant communities, and generally show that the presence of earthworms favours the growth of fast-growing grass species over forbs and legumes (Hopp and Slater, 1948; Scheu, 1987; Wurst et al., 2005). The mechanism is still unknown but it is likely to relate to a positive effect of earthworms on soil N availability that in turn promotes the growth of grasses. Grasses may also benefit from the more patchy distribution of organic matter in soils with earthworms, since grasses tend to be better able to forage resource through root proliferation than are forbs and legumes (Scheu, 2003). Earthworms are also able to influence the seedling recruitment in grasslands, especially of annual weeds through the selective feeding and transport of seeds (Pierce et al., 1994; Jolivet, 1996). We are aware of only few studies about the significance of these processes in natural plant communities, but it is likely that feeding preferences and transport of seeds, and modification of germination by earthworms substantially strongly influence plant community structure (Decaëns et al., 2003).

Hence, soil accidental engineers can also affect heterogeneity at both the biogenic structures and landscape scales, in affecting vegetation growth and diversity where engineers are active. Once again, the consequences of these modifications for the fitness of accidental engineers is difficult to determine but would be of primary interest for understanding the direct and indirect links between the ecological requirements of soil accidental engineers and their effects on ecosystem functioning.

CONCLUSION

The patch-matrix model appears to be the dominant conceptual model used in soil ecology. This model has many limitations in ecosystem science and management. The aim of this paper was to emphasize the overwhelming complexity of interactions between ecosystem engineers, their environment, the size and frontiers of their functional domains and ecosystem structure (composition and configuration). We tried to show in this paper how difficult it is to highlight all the functional roles play by heterogeneity maintained by soil engineers and also to delimit the frontiers of biogenic structures. Ecosystem functions that are affected by heterogeneity include maintenance of species diversity (habitat) as well as material and energy cycles. Hence, further researches are now needed to indicate the magnitude and impact of ecological processes involved by soil engineers and to build predictive models that could be used for ecosystem managements.

Surprisingly, few studies have focused on how soil engineers affect spatial and temporal heterogeneity and hence ecosystem functioning and how their ecology (accidental vs. extended phenotype engineers) regulate these processes. There are some of the major questions which need to be answered to develop a more complete understanding of the influence of soil engineers on heterogeneity pattern and ecosystem functioning and to help us to conceptualize and determine explicit models of spatial heterogeneity in ecosystem processes. We only start to be able to tackle the issue of the effect of spatial heterogeneity and its interaction with ecosystem engineers on ecosystem functioning. Without these kinds of knowledge, our efforts to control ecological processes with soil engineers may have unintended and unfortunate consequences for biodiversity and ecosystem function. Indeed, particular attention must be taken to not introduce soil engineers to a system where they would proliferate and become pests or damage the soil system (Chauvel et al., 1999).

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