

# Ecosystem stability and resilience: a review of their relevance for the con- servation management of lowland heaths

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## Abstract

Ecosystem stability and the response of ecosystems to disturbance are of crucial importance for conservation management, especially when the object is to maintain and/or to restore early-successional communities. This paper provides a selective review of ecosystem stability from a conservation perspective. Existing models of ecosystem resilience are discussed in relation to the management of successional habitats. A multivariate model for measuring stability and resilience based on Canonical Correspondence Analysis (CCA) is outlined. The criteria for the model to work are explained and the model is tested on vegetation and soil data from the Dorset Heaths. The model provides a mechanism for bringing together measurements of both structure (species composition) and function (ecosystem properties, both biotic and abiotic), to measure stability and resilience of ecosystems. The model can also be used to measure the success of management in restoring communities and to provide information to conservation policy makers and land managers.

**Key words:** CANOCO, resilience, resistance, ecosystem stability, conservation management, heathland conservation

## Introduction

Ecosystem stability has been the subject of many debates in ecology, often from a theoretical perspective. Yet ecosystem stability and the response of ecosystems to disturbance are of crucial importance for conservation management, especially when the objective is to maintain and/or restore early-successional communities. These communities need the intervention of man to maintain them at quasi-equilibrium and prevent succession towards another state. Where succession has

already occurred on sites where an earlier successional state is desired, then intervention is needed to re-establish the community required by the conservation policy makers.

When any conservation management is applied there is a need to know: Whether it is working or not? How stable the managed community is? Whether the community can be held at a defined position in the succession? How quickly it will change between states? – The answers to these questions are essen-

tial, not only to put conservation science on a sounder ecological footing, but also to:

- develop techniques to measure success/failure of management,
- to target the most appropriate management problems,
- to use management resources to best effect,
- to have an objective scale to measure ecosystem change.

In this paper we provide a selective review of ecosystem stability from a conservation perspective, and suggest a possible methodology for measuring stability and resilience during conservation management of sub-seral communities undergoing succession. We use as case study the lowland heaths in Dorset, UK, an internationally important biotope (Department of Environment 1995a, b).

#### **Ecological justification for conservation management: the conflict between intervention and non-intervention**

There is a potential conflict between two possible approaches to the conservation of sub-seral communities, whether to take a non-intervention or an intervention approach. When a non-intervention approach is adopted there will almost certainly be a loss of the sub-seral communities, at least temporarily as succession occurs (Fig. 1a). However, it could be argued that the communities are transient within a succession, and they will recur throughout the landscape sporadically as the late-successional stages either die-back or are removed due to natural disturbances (Fig. 1b).

This approach depends on several factors. On the one hand, there must be a large area of land available in which patch dynamics at a range of both temporal and spatial scales can operate to provide a continual supply of disturbed land on which succession can occur. On the other hand, the species involved must either have dispersal properties that allow their movement between these patches, or they must have long-term propagule banks.

The interventionist approach is more direct; here there is a planned disturbance to maintain examples of the sub-seral community within relatively tight successional constraints (Fig. 1c). Deliberate management of late-successional communities to restore early-successional communities may also be

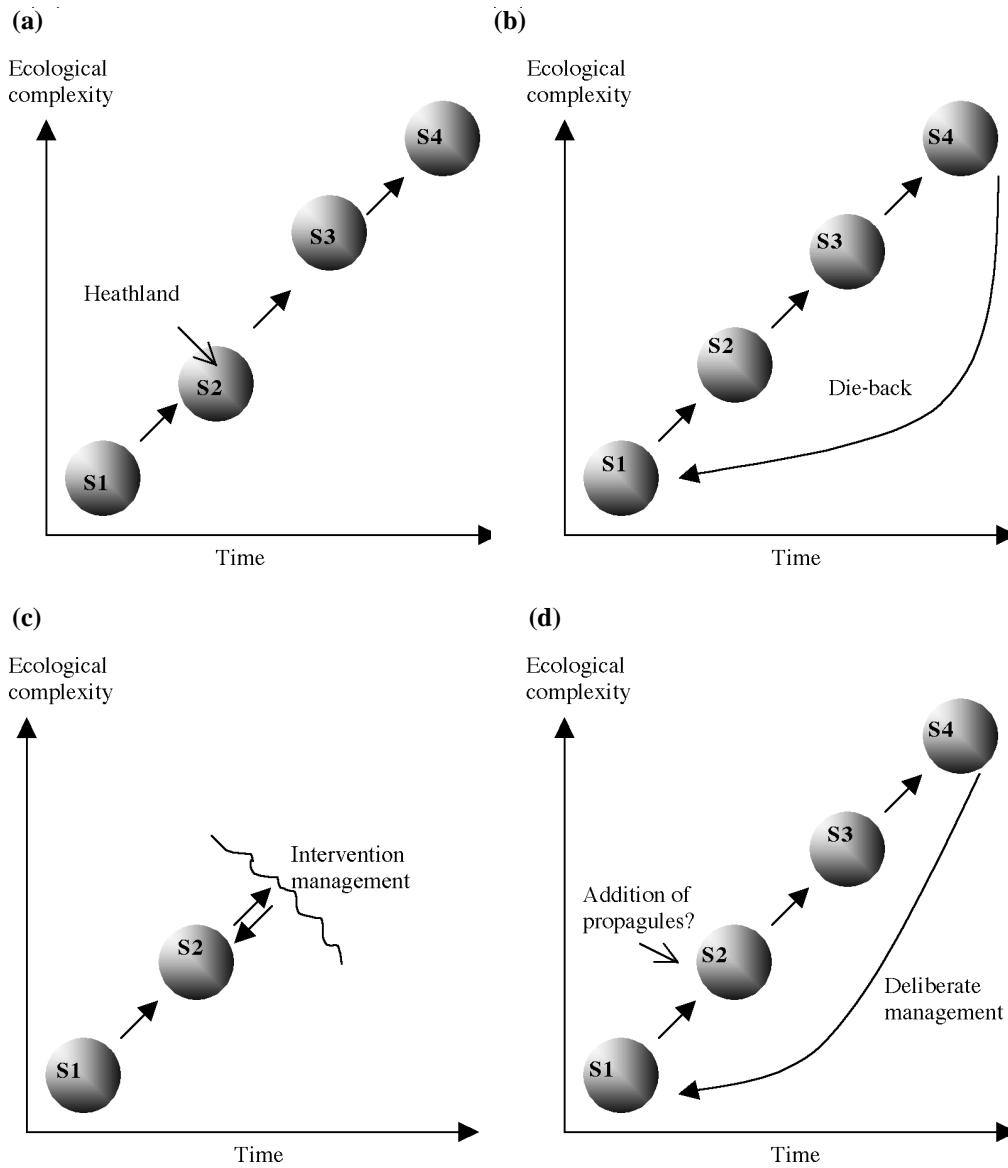
applied, with the possible addition of propagules to aid the establishment of the desired community (Fig. 1d).

In the UK, an interventionist policy has been adopted for the conservation of many sub-seral biotopes, including chalk grasslands, heathlands and reedbeds. The reasons for this are complex but include the small size and fragmented nature of many of the remnant sites on which these biotopes persist (often protected sites are less than 100 ha; Ratcliffe 1977), the desire to maintain representative examples of rare species and their communities, and international obligations to conserve important biotopes (Department of the Environment 1995a,b). Lowland heathlands are one example of a biotope that is well represented in the UK. It is acknowledged as a high priority for conservation on the basis that it supports many species that are rare or endangered. In the UK much lowland heath has been lost to other land use types over the last 200 years (Moore 1962; Farrell 1993; Webb & Haskins 1980; Rose *et al.* 2000), and the remainder has often been poorly managed with the loss of pristine heathland to late-successional communities. The aim of conservation policy makers has been to provide some form of designated protection to remaining lowland heath sites, and thereafter to maintain existing heathland through positive action, and extend it where possible by restoring heath on areas lost through succession.

A good example of this policy in action are the lowland heaths in Dorset. These heathlands have been reduced in extent from 30,000 ha in 1811 (Moore 1962) to 5141 ha in 1987 (Webb 1990). In 1989 "The Dorset Heathland Project" was established by the Royal Society for the Protection of Birds (RSPB). This conservation management programme aimed to increase the amount of open heathland in Dorset by a programme of habitat restoration, targeting its work to reduce fragmentation as much as possible. In the first five years of the project 433 ha of heathland were restored and heathland management was carried out on a total of 522 ha (Woodrow *et al.* 1996a).

#### **Management of lowland heaths in Dorset**

The Dorset heaths, like heathlands elsewhere, are dominated by slow-growing, ericaceous sub-shrubs. The dry heaths are



**Fig. 1.** Differences between an interventionist approach and a non-interventionist approach in relation to successional communities and maintaining sub-seral communities. (a) The non-interventionist approach leads to the loss, at least temporarily, of sub-seral communities; (b) the non-interventionist approach may lead to the re-occurrence of sub-seral communities following die-back of late-successional stages; (c) the interventionist approach maintains the sub-seral community within relatively tight successional constraints; (d) the interventionist approach deliberate management of late-successional communities to restore early-successional communities. S1-S4 are successional stages.

dominated by *Calluna vulgaris* with *Erica cinerea* and *Ulex minor* or *Ulex gallii*. The most common grass is *Agrostis curtisii*; on the wetter heaths *Erica ciliaris* and *Erica tetralix* occur together with *Molinia caerulea* (Webb 1986). The heaths occur on very nutrient-poor soils and any increase in nutrient supply tends to increase the rate of successional change. Originally, these heaths were used by the local rural population for sheep grazing, turf cutting, firewood collection, and removal of bracken and litter for animal bedding. The heaths were an integral part of the local agricultural system (Webb 1998), which maintained the sub-seral heathland community and stopped succession occurring. As a result of changes in agricultural practises, succession has occurred and a range of woody trees and shrubs have invaded, including *Betula* spp., *Pinus sylvestris*, *Pteridium aquilinum* and *Rhododendron ponticum* (Mitchell *et al.* 1997). The types of conservation management applied today to maintain heathlands include cutting and burning at appropriate stages in the growth cycle of *Calluna* (Gimingham 1992). To restore heathland communities on successional sites various management techniques are used, including: clear-felling and timber removal, herbicide treatment, litter removal and introduced grazing (Auld *et al.* 1992; Byfield & Pearman 1995; Woodrow *et al.* 1996a,b).

### Ecosystem stability – a theoretical perspective

The stability of ecosystems is the subject of many debates with many models produced (Jordan *et al.* 1972; May 1973; Harrison 1979; DeAngelis 1980; Pimm 1984; Nakajima & DeAngelis 1989; Naeem 1998), which aim to predict what makes an ecosystem stable and the effects of disturbances on that ecosystem. Ecosystem stability is conventionally defined in two parts, its *resilience* and its *resistance* (Webster *et al.* 1975; Leps *et al.* 1982). Ecosystem resilience is the ability of the system to return to normal after a disturbance or stress period; this is consistent with the definition of Webster *et al.* (1975), Leps *et al.* (1982) and Pimm (1984, 1991), although May (1973) and Holling (1973) call this concept stability. The greater the resilience of an ecosystem the shorter its recovery or return time to equilibrium ( $Tr$ ) following a perturba-

tion; resilience is therefore measured as  $1/Tr$ . Resistance is the ability of the system to avoid displacement during periods of disturbance in its environment (Leps *et al.* 1982); although Holling (1973) refers to this property as resilience. Here resilience and resistance are used according to the definitions above.

Most studies of ecosystem resilience start from the premise of assuming that the ecosystem will return to the same equilibrium after disturbance. Ecosystems with a high resistance to perturbations and high resilience are therefore most stable and are thus easiest for land managers to maintain. However, ecosystems with a high resilience or high resistance can be problematic for conservation managers when the management aim is to deliberately change a stable ecosystem from one state to a different state, i.e. when management aims to reset the succession at an earlier stage.

Before reviewing different models for assessing stability and response to change it is worth noting that stability *sensu stricto* is only a valid concept when there is an implicit assumption that the ecosystem is stable and at equilibrium. This is unlikely to be strictly true as all ecosystems are dynamic and therefore in constant change (Miles 1979; Williamson 1987); they are also surrounded by a stochastic environment (May 1973) that is itself continuously changing (Holling 1996a). For a sub-seral community it is extremely unlikely that it will be stable in the long term, unless extreme climatic conditions mean that the climax succession is unable to develop. Stability is scale dependent and human spatial and time scales strongly influence what we perceive as stable. However, the concept of ecosystems as a quasi-equilibrium is a useful starting point for theoretical studies of ecosystem stability. Indeed, some ecosystems may have more than one stable equilibrium and may flip between them after disturbances or following degradation of the ecosystem (Holling 1996b). Management work to establish an earlier successional community may cause the ecosystem to flip to a new equilibrium, which may or may not be the target desired by the land managers.

### Current models for studying ecosystem stability and response to disturbance

The stability of an ecosystem is usually measured either by vegetation structure (bio-

mass/cover of component species) or by a measure of ecosystem function (nutrient cycling). This is an over-simplification because for any biotope the vegetation and soils are only two components; a complete assessment would need to include component fauna, e.g. invertebrates, birds, animals, reptiles, decomposers and micro-organisms. In restoration studies these must also be considered but in order to achieve any ecological resilience the vegetation and soil must be established first. This paper therefore concentrates on the resilience of successional ecosystems in terms of the appropriate soil conditions and vegetation, and ignores other components of the ecosystem. We accept this is a simplification, but for lowland heaths these are two of the most important components.

### Species diversity and ecosystem resilience

Species diversity is often cited as a key feature of ecosystem resilience (Hurd *et al.* 1971; Leps *et al.* 1982; Virágh 1989; Frank & McNaughton 1991; Baskin 1994; Naeem *et al.* 1994; Tilman & Downing 1994; Collins 1995; Dodd *et al.* 1995; McGillivray *et al.* 1995; Tilman *et al.* 1996). However, there is considerable debate over whether species diversity is an impartial factor controlling resilience. Some studies show a positive correlation between the two (McNaughton 1978; Tilman 1984), others show an increase in resilience up to an asymptote (Baskin 1994; Stone *et al.* 1996), yet others show no increase in resilience, although possibly more resistance (Leps *et al.* 1982).

#### Diversity and stability – theoretical models

Four hypotheses about the role of species diversity in contributing to ecosystem stability have been proposed (Johnson *et al.* 1996). The *diversity-stability hypothesis* predicts that as species diversity increases so too does ecosystem productivity and resilience (MacArthur 1955). The *rivet hypothesis* likens the species in an ecosystem to rivets in an aeroplane (Ehrlich & Ehrlich 1981); the removal of rivets (species) beyond a certain number will cause the aeroplane (ecosystem) to crash catastrophically. This suggests that the ecosystem will continue to function normally if there are only a few extinctions but

the loss of a critical species or number of species may cause instability within the ecosystem. The *redundancy hypothesis* proposes that certain species are able to expand their role in the ecosystem to compensate when neighbouring species are lost (Walker 1992). This implies that species are segregated into functional groups and species in a given group can expand to fulfil the role of other species in the same functional group should some become extinct. This hypothesis has recently been expanded by Peterson *et al.* (1998) who propose that the resilience of ecological processes, and therefore of the ecosystems they maintain, depends upon the distribution of functional groups within and across scales. They hypothesise that if a functional group contains species that operate at different scales they are likely to be more resilient. The *idiosyncratic hypothesis* proposes that although ecosystem function changes when diversity changes, the magnitude and direction of the change is unpredictable because of the complexity of the ecosystem and the varied response of the species (Lawton 1994).

#### Relevance of these models to lowland heaths

The type of model operating will affect the ease with which different late-successional communities revert to early-successional communities. The restoration of heathland on late-successional sites will be most successful when the late-successional communities have low resilience. With information on the above models and the species composition of the late-successional sites it should be possible to predict which communities will be easy to restore to heathland and which will be hard. When these predications are compared to practical experience of managed sites it is possible to suggest whether or not these models are operating on the Dorset Heaths (Table 1). Throughout this paper a "managed sites" refers to a site with a late-successional community that received a one off management treatment, e.g. clear-felling trees, with the aim of re-establishing heathland vegetation.

If the diversity-stability hypothesis operates, then sites, where a single species takes over to the exclusion of all other species, will be easier to restore to a species-rich plagioclimax community, than sites where succes-

**Table 1.** Prediction of which successional stages on lowland heathland would be easiest to restore to heathland, if four different hypotheses about ecosystem stability were operating compared to actual conservation experience (B, *Betula* spp. successional sites; PS, *Pinus sylvestris* successional sites; PA, *Pteridium aquilinum* successional sites; R, *Rhododendron ponticum* successional sites).

Ease of restoration	Hypothesis					Actual conservation experience (as given in Mitchell <i>et al.</i> 1999)	
	Diversity-stability	Rivet		Redundancy	Life strategy		
Easy ↓	R	} All equally easy to restore	}	PS	PS	PS	
	PS, PA			B, PS	R	PA	PA
	PA			PA, R	PA	B	R
Hard	B				B	R	B

**Table 2.** The number of heath and non-heathland species present on ten Dorset heaths and corresponding successional sites.

Ease of restoration to heathland (as given in Mitchell <i>et al.</i> 1999)	Successional stage	Number of heathland species	Number of non-heathland species	Total number of species
Easy ↓	Heath	26	2	28
	<i>Pinus sylvestris</i>	17	8	25
	<i>Pteridium aquilinum</i>	15	19	34
	<i>Rhododendron ponticum</i>	13	9	22
	Hard	<i>Betula</i> spp.	15	21

sion increases the number of species. Thus, on the Dorset heaths *Pinus sylvestris* successional sites that contain fewer species than *Betula* spp. sites (Table 2) should be easier to restore to heathland (Mitchell 1997). Indeed, in the majority of the managed successional sites studied on Dorset heaths heathland re-establishment was more successful on managed *Pinus sylvestris* sites than managed *Betula* sites (Mitchell *et al.* 1999), suggesting that this theory might be operating on these sites. However, the *Rhododendron ponticum* successions had fewer species than the *Pinus sylvestris* sites yet these were generally harder to restore to heathland (Mitchell *et al.* 1999).

If the rivet hypothesis operates then the easiest sites to restore will be successional sites where there are only a few key species and the removal of these is all that is needed for successful restoration. Thus identification of the key species within a successional site is essential for successful restoration. For successional sites we assume that the key species would be the dominant invader (e.g. *Betula*, *Pinus* etc.). According to the rivet hypothesis the varying success rates of heathland restoration clearly show that there are

more key species than just the dominant invader.

If the redundancy hypothesis operates, sites with a mixture of successional species will be harder to restore to heathland than sites with few successional species present. The *Betula*, *Rhododendron* and *Ulex* sites have more non-heathland species present than the *Pinus sylvestris* sites which are generally easier to restore (Table 2). However, *Rhododendron* sites which are generally hard to restore to heathland also have few non-heathland species present.

If the idiosyncratic hypothesis operates then it will be impossible to predict which sites will be easier to restore.

The data therefore indicate that although some of these hypotheses may hold for some successional sites, no hypothesis holds for all successional sites. The differences between restoration success may of course also be due to differences in unknown interactions between species and other factors, for example soil nutrient status and species life history strategy. Key species in late-successional communities may have influenced habitat factors, such as soil nutrients, affecting the ease/difficulty of restoration.

### Resilience and life strategy

Leps *et al.* (1982) hypothesised that resistance and resilience in old field successions could be explained using species strategies *sensu* Grime (1979). Communities composed of mainly competitive-ruderals had lower species diversity, lower community resistance and higher community resilience, whereas communities mainly of stress tolerators and C-S-R strategists had higher species diversity, high community resistance and lower community resilience. MacGillivray *et al.* (1995) tested this hypothesis and showed that tolerance of nutrient stress was positively correlated with resistance to initial damage and negatively correlated with resilience.

Successional communities that contain more competitive species may, therefore, be more difficult to restore to heathland as these communities will have a greater resilience and are therefore more likely to re-establish quicker than communities composed of stress tolerators. In plagio-climax communities such as heathlands and chalk grasslands where the communities contain many stress-tolerant species the resilience of the late-successional communities containing many competitive species could be problematic. This has been suggested as a problem in the restoration of heathland on *Betula* sites (Mitchell *et al.* 1997), which contain more

competitive species than for example *Pinus sylvestris* sites.

Table 3a shows that there are more non-stress-tolerant species on the successional sites than on the heath sites. The successional stages show no relationship between the number of stress-tolerant species present and the ease of heathland restoration. Table 3b compares the mean cover of each life history category for heathland and successional communities on one of our test sites (Arne). This shows a decrease in the cover of stress tolerators and an increase in the cover of competitors as the success of management in restoring heathland declines. Table 3 includes only the vascular plants present in the communities; however, it suggests that differences in the abundance of stress-tolerant species between successional communities may be related to the resilience of that community.

### Resilience and ecosystem function

Nutrient cycling has often been used as a measure of stability. Odum (1969) hypothesised that as succession proceeds nutrient cycling becomes tighter, resistance increased and resilience decreased. Evidence supporting this comes from Webster *et al.* (1975), DeAngelis (1980) and Loreau (1994)

**Table 3.** Classification of vascular plant species occurring on heathland and successional sites by life strategy *sensu* Grime *et al.* (1988) (? , life strategy unknown).

Ease of restoration to heathland (as given in Mitchell <i>et al.</i> 1999)	Successional stage	Life history strategy			
		S/SC/SR	C/CR/CS	CSR	?
(a) Numbers of species at different successional stages on ten heathland sites and corresponding successional sites in Dorset.					
Easy ↓ Hard	Heath	7	1	0	2
	<i>Pinus sylvestris</i>	6	2	0	3
	<i>Pteridium aquilinum</i>	13	3	6	3
	<i>Rhododendron ponticum</i>	9	1	1	1
	<i>Betula</i> spp.	13	4	3	2
(b) Comparison of mean cover of different life strategies on heathland site and successional communities at one site (Arne) in Dorset.					
Easy ↓ Hard	Heath	94.3	0	0	0.4
	<i>Pinus sylvestris</i>	36.3	0.3	0	0
	<i>Pteridium aquilinum</i>	68.7	0.75	0.02	0
	<i>Rhododendron ponticum</i>	4.3	90.12	1.7	0
	<i>Betula</i> spp.	2.4	44.1	0.65	0

who consider that ecosystems with a strong degree of recycling are likely to be less resilient. However, although nutrient cycling generally becomes tighter during succession, when losses of nutrient are low the losses may increase again in late-successional stages (Vitousek & Reiners 1975). In most studies the nutrient content of the plants (nutrient concentration  $\times$  biomass) or loss of nutrient in the stream flow have been monitored and used as examples of ecosystem function. Few studies have considered soil chemistry or functions that control plant growth.

Bormann & Likens (1979) monitored the accumulation of total biomass and the loss of nutrients from the system into the stream water in logged and forested watersheds in a northern hardwood forest during successive years. The model contained four phases of development following logging. First, a *Reorganisation Phase* during which there was a loss of biotic control with a loss of total biomass and increased losses of soil nutrients into the stream water as the closed and presumably tight nutrient cycle was broken (Odum 1969). The second was the *Aggrading Phase*, where the nutrient cycle was highly regulated by biotic and abiotic components of the ecosystem and the total biomass reached a peak at the end of this period. Next was the *Transition Phase*, where total biomass declined from its peak at the end of the *Aggrading Phase* till it reached a *Steady-State Phase* where the nutrient cycles are well regulated and the biomass fluctuates around a mean.

Vitousek & Reiners (1975) in a similar study proposed a similar model with rapid loss of nutrients following logging. However, after the initial disturbance the rate of nutrient loss depended on the importance of the nutrient to plant growth. Growth-limiting nutrients were retained most strongly and decreased in output with time; elements that are essential, but not limiting, were retained but outputs were greater than for those of growth-limiting nutrients; and finally outputs of non-essential elements varied little over the course of succession. Outputs of the limiting and essential elements started to increase again once the rate of net biomass increase started to decline. Thus, the resilience of the nutrient recycling is dependent on the type of nutrient; non-essential nutrients tend to be more resilient than essential nutrients (Jordan *et al.* 1972). Losses of nutrients from a system may vary over the course of succession, being

high at the beginning of secondary succession, declining during mid-succession and increasing again in late-successional stages.

As succession proceeds soil nutrient concentrations may increase (Miles & Young 1980; Miles 1985), either by accumulation through time or through positive feedback mechanisms. When this occurs there will be important implications for the reversal of succession. On the Dorset Heaths increases in different soil nutrients have been associated with different successional species and related to the ease of restoring heathland (Mitchell *et al.* 1997, 1999). After removal of the successional species the raised soil nutrient levels may allow more competitive species to re-establish to the detriment of slower growing, stress-tolerant species (often the target species for re-establishment). Alternatively, the whole successional process may be accelerated and successional communities quickly re-establish (Marrs & Gough 1989; Marrs 1993). Thus, the resilience of the nutrient cycling system within the ecosystem will have important implications for the success of the restoration of early-successional communities on late-successional sites. If there is low resilience, then the increased levels of soil nutrients may be quickly lost from the system thus helping to re-establish an early-successional community. However, if resilience is high and the increased soil nutrients are maintained within the system then late-successional communities may quickly re-establish.

### Relevance of these existing models for conservation management

The models discussed above are either based on attributes of ecosystem structure (species presence/absence) or ecosystem function (nutrient cycling). There have been few attempts to combine both of these attributes. Moreover, the ecosystem structure models have been extremely difficult to apply to conservation management data collected from the Dorset heaths except in a very crude, broad-brush way. They would be more or less impossible to be used by conservation managers in real situations to provide informed opinion on either the state of the management or target assessment. To collect information on nutrient budgets would be beyond the scope of most conservation management programmes, as finance would not



be available and the skills are not routinely available.

## A multivariate modelling approach

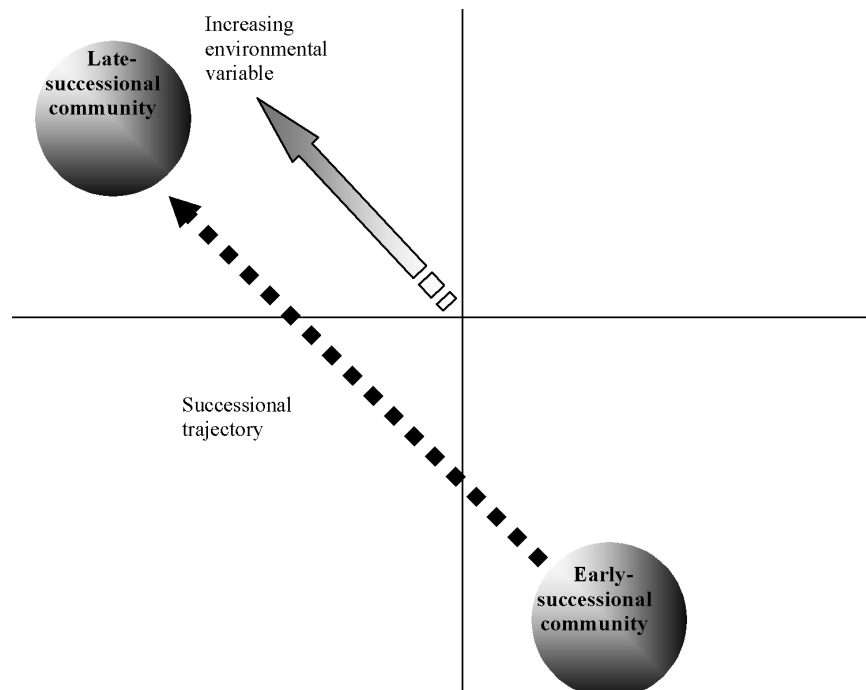
### Background

Here, we outline a multivariate modelling approach developed by Mitchell *et al.* (1997, 1999) and tested on these Dorset Heaths. This model combined measurements of species and other environmental variables, which can either represent attributes of ecosystem structure or function. In the Dorset heaths both biotic (vegetation structure) and abiotic (soil nutrients function) factors were included; the soil factors were selected as they are known to have a major impact on both conservation status and management success (Gimingham 1992). Whilst we have included only soil parameters in the first instance, we accept that other factors may need to be included in improved versions. Some parts of the ecosystem may be more

resilient than others (Westman 1978), and hence it may be impossible to measure the resilience of an ecosystem based on one property alone (Virágh 1989); a multivariate model overcomes this problem.

The model is based on constrained multivariate ordination using Canonical Correspondence Analysis (CANOCO, Ter Braak 1988). This approach allows species abundance and environmental variables to be analysed simultaneously and then displayed in an ordination diagram, with the sites/plots and species plotted in ordination space on the axes that are associated with increasing environmental variables, usually shown as arrows.

At the present time the development of this approach is in its infancy. So far we have only managed (1) to rank late-successional vegetation types with respect to their multivariate "closeness to the target heath communities", with the implication that communities close to the heathland community will be easier to restore, and (2) to assess the performance of conservation management in relation to whether the vegetation change is



**Fig. 2.** A simplified CANOCO type model illustrating how successional trajectories might be shown between late- and early-successional communities, and how changes in environmental variables may also be illustrated.

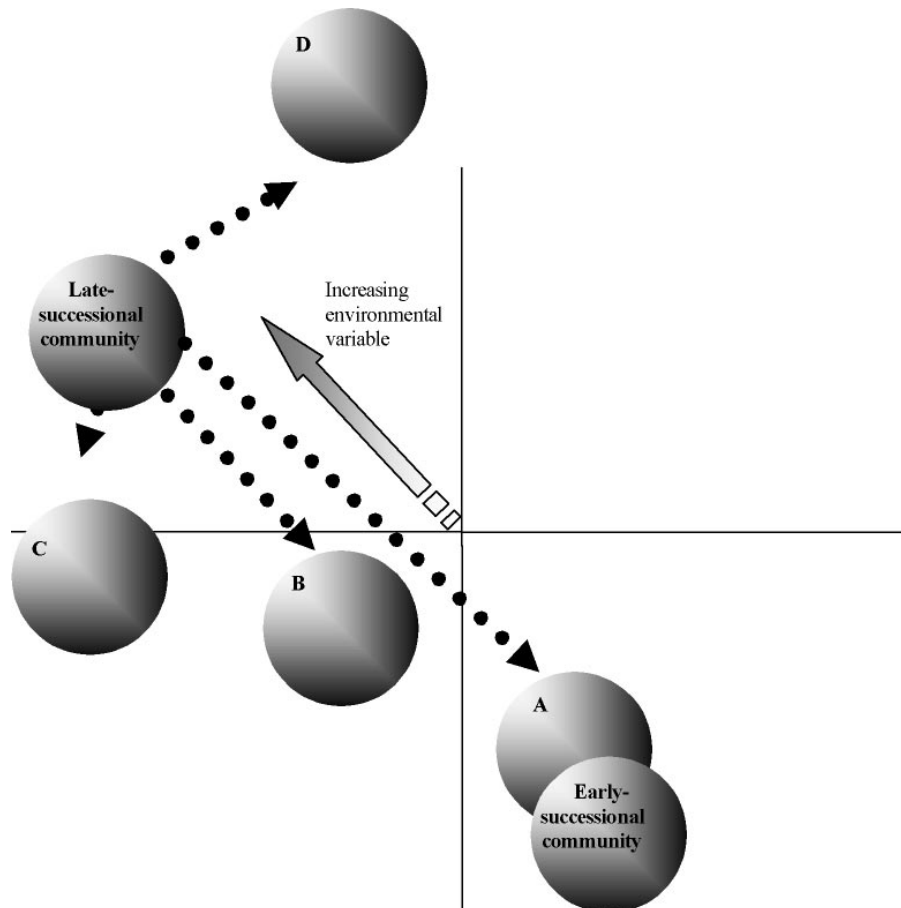
going in the correct direction and how close the management is to achieving its target. Throughout it has been possible to derive quantitative measures that could be used directly by conservation managers to assess success and, if repeated, to chart progress. However, in order to derive measures of ecosystem resilience the approach would have to be repeated over the course of a relatively long-time span, probably 5 to 10 years.

### Outline of the modelling approach

Figure 2 shows a simplified CCA diagram where an early-successional community is moving towards the late-successional community with a particular environmental variable increasing. In this example the management aim would be to move the late-succes-

sional site back towards the early-successional community. Assuming that information could be collected for both vegetation types for a long enough period it would be possible to measure:

- (1) the resistance of both the early- and late-successional sites, i.e. how much management force is needed to move the late successional site away from its quasi-equilibrium and how much natural "successional pressure" is operating on the early-successional sites;
- (2) the rate of change enforced by management;
- (3) the resilience of the managed site, i.e. how quickly does the late-successional community re-establish following a one-off management treatment.



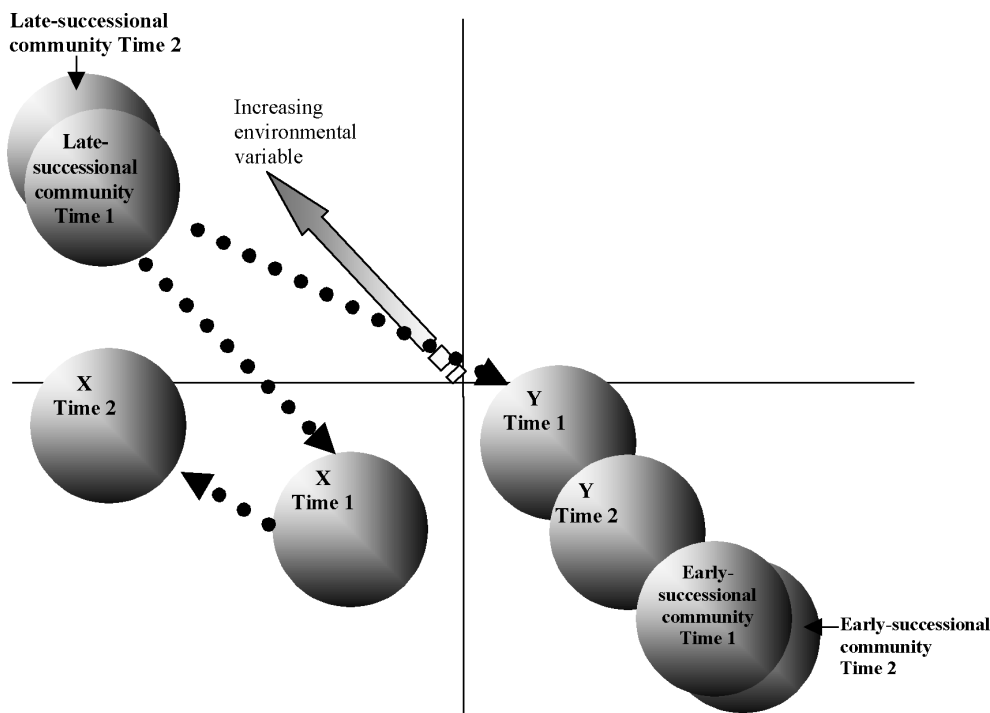
**Fig. 3.** Measuring management success using a CANOCO type model. The movement of four different managed sites (A, B, C, D) in relation to the early- and late-successional communities.

Management to restore early-successional communities on late-successional sites may be more successful on some sites than on others (Fig. 3). Some sites may become similar to the early-successional communities (Fig. 3, site A). Other sites may start to move towards the early-successional communities but not get there as quickly (Fig. 3, site B). Thirdly, a site may remain similar to the late-successional communities despite management (Fig. 3, site C), and finally the management may cause the site to move towards a totally different community other than the one desired (Fig. 3, site D).

Repeat measurements can show any movement (or change) in sites whether at an early- or late-successional stage. This may be used to test the assumption that a given site is at equilibrium (Fig. 4). Repeat measurements will also allow the resilience of the ecosystem to be measured. The success of the management will depend partially on the

resilience of the late-successional site. If the site has high resilience then late-successional species will quickly re-establish on the site and the managed site will move back towards the late-successional communities (Fig. 4, site X), such sites will require both resources and conservation effort to be maintained as early-successional sites. If the site has low resilience (Fig. 4, site Y) then the site will be relatively easy to maintain as an early-successional community.

The results from this approach are not only of theoretical importance, they answer the questions that conservation managers need answered. The use of CCA to test these simple models allows a rapid, quantifiable and independent assessment of success/failure of conservation management and allows performance to be tested. This can be done graphically as illustrated in Fig. 3 and also by measurement of inter-site distances in the CCA model.



**Fig. 4.** Measuring resilience using a CANOCO type model. The movement of two managed sites (X, Y) after a one-off management treatment are plotted for two different times. Site X has high resilience and quickly starts to move back towards the late-successional community following management; site Y has low resilience and continues to move towards the early-successional stage following management. The movement of the late-successional and early-successional sites between time 1 and time 2 shows how the model may be used to test if a site is at equilibrium.

There are still some difficulties in terminology: the concept of resistance of late-successional communities may be questioned. When management is severe, for example when sites are clear-felled and the vegetation removed, the species cannot contribute further to the system properties; however where perennial species such as *Pteridium aquilinum* are cut then resistance is a function of *Pteridium aquilinum* recovery and would be relevant. These difficulties however are outweighed by the advantages of this approach as the model:

- tests the assumption that the ecosystem is at an "approximate equilibrium";
- tests the assumption that the disturbed ecosystem will return to an approximation of its undisturbed state;
- provides a mechanism for bringing together measurements of both structure (species composition) and function (ecosystem properties, both biotic and abiotic);
- provides a measure of the variability within the ecosystem under investigation (for practical resource management this should be independent of scale and operate at the individual site level, but allows expansion to cover biotopes at regional, national and total scale);
- can accommodate unforeseen ecosystem change associated with stochastic or other factors;

- is statistically rigorous and able to determine which environmental variables are most important for describing the system;
- is useful in practical resource management.

## Testing the model on lowland heaths

### Methodology

We tested this CCA modelling approach on the lowland heaths of Dorset. Two surveys were carried out. The first in 1995 involved only early-successional communities (heath) and late-successional communities (Mitchell *et al.* 1997). Aerial photographs of the sites in 1946/47, 1972/73 and 1986 showed that the late-successional communities were all covered with heathland vegetation 20–50 years ago (Mitchell *et al.* 1997). The successional communities were classified by the dominant species invading. The second survey (Mitchell *et al.* 1999), carried out a year later included managed sites as well as a repeat survey of many of the early- and late-successional communities surveyed in the first survey. Managed communities were late-successional habitats, which had been managed between 1–10 years ago with the aim of restoring heathland on them. The management usually consisted of a one-off treatment, e.g. clear-felling and removal of trees/

**Table 4.** The stages present at each area and the number of sites sampled within each stage; ten samples were taken at each site. National Grid References for the areas are also shown (reproduced from *Journal of Applied Ecology*, **36**, 770–783). Four successional stages were sampled: +B, major invader is *Betula* spp.; +PS, major invader is *Pinus sylvestris*; +PA, major invader is *Pteridium aquilinum*; +R, major invader is *Rhododendron ponticum*. For each of these stages there were corresponding managed sites where the succession had been managed in an attempt to restore heathland, namely: mB, managed +B; mPS, managed +PS; mPA, managed +PA; and mR, managed +R.

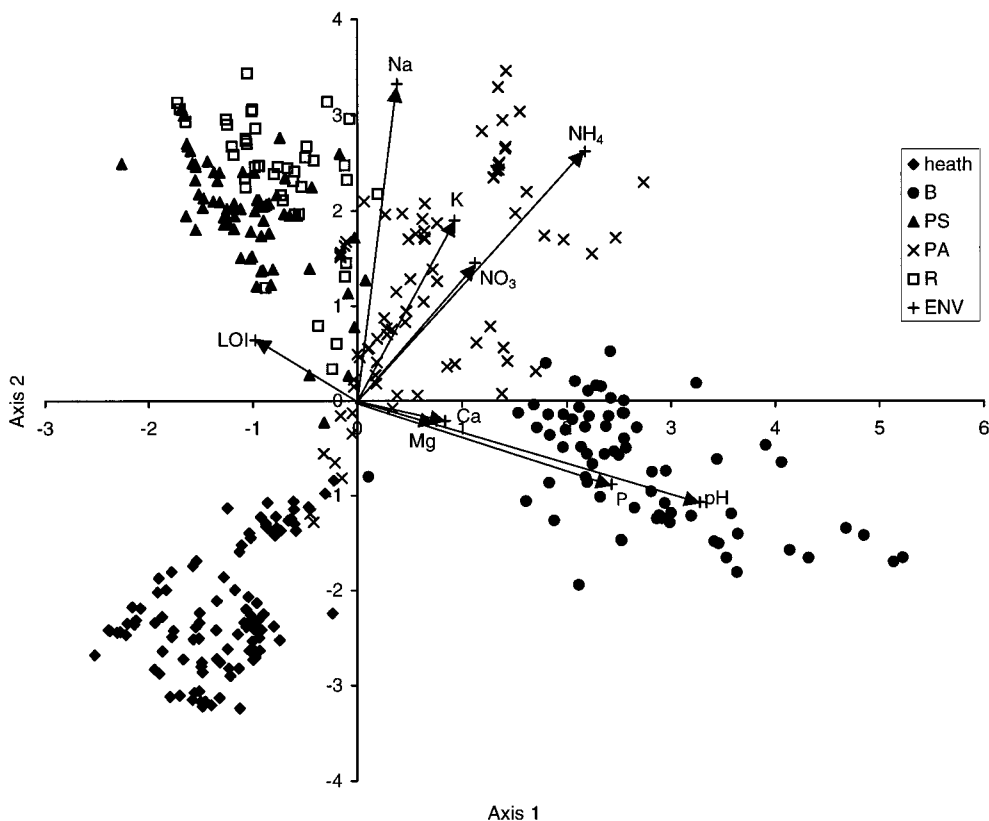
Area	National grid ref.	Stage								
		Heath	+B	mB	+PS	mPS	+PA	mPA	+R	mR
Arne	SY973882	1			1	5	1	1	1	1
Avon Heath (AHCP) Country Park	SU128035	1	1	1	1	2				
Blackhill	SY840940	1			1	1	1	2	1	1
Cranborne Common	SU104112	1					1	1		
East Holton Heath	SY958917	1			1	2				
Grange Heath	SY909835	1			1	1				
Merritown Heath	SZ113991	1	1	1	1	1				
Sopley & Ramsdown	SZ133974	1	1	1	1	1			1	2
Trigon Heath	SY884908	1	1	1	1	1	1	1	1	1
Total no. sites		9	4	4	8	14	4	5	4	5
Total no. samples		90	40	80	140	40	50	40	50	

bushes and occasionally litter, however management of *Pteridium aquilinum* required repeated management (spraying or cutting) over several years. Details of the management and sites can be found in Mitchell *et al.* (1999). In both surveys a range of sites across the Poole Basin in Dorset was studied each containing a heathland community and a range of late-successional habitats (Table 4). The vegetation was surveyed and the cover of all species recorded in a series of random quadrats. A soil sample was taken from the middle of each quadrat and analysed for extractable ammonium-N, nitrate/nitrite-N, exchangeable calcium, magnesium, sodium and potassium. The pH of the soil was measured and the organic matter con-

tent of the soil estimated by recording the loss-on-ignition. Soil nutrients were chosen as the environmental variables to be included in the model as heathlands are known to occur on poor soils (Gimingham 1992), and elevated soil nutrient concentrations are known to affect heath vegetation (Heil & Diemont 1983; Aerts & Berendse 1988; van der Eerden *et al.* 1991). The results from both the surveys were analysed by Canonical Correspondence Analysis (Ter Braak 1988).

### Successional changes

The results from the first survey (Fig. 5) reported in detail in Mitchell *et al.* (1997) showed that:



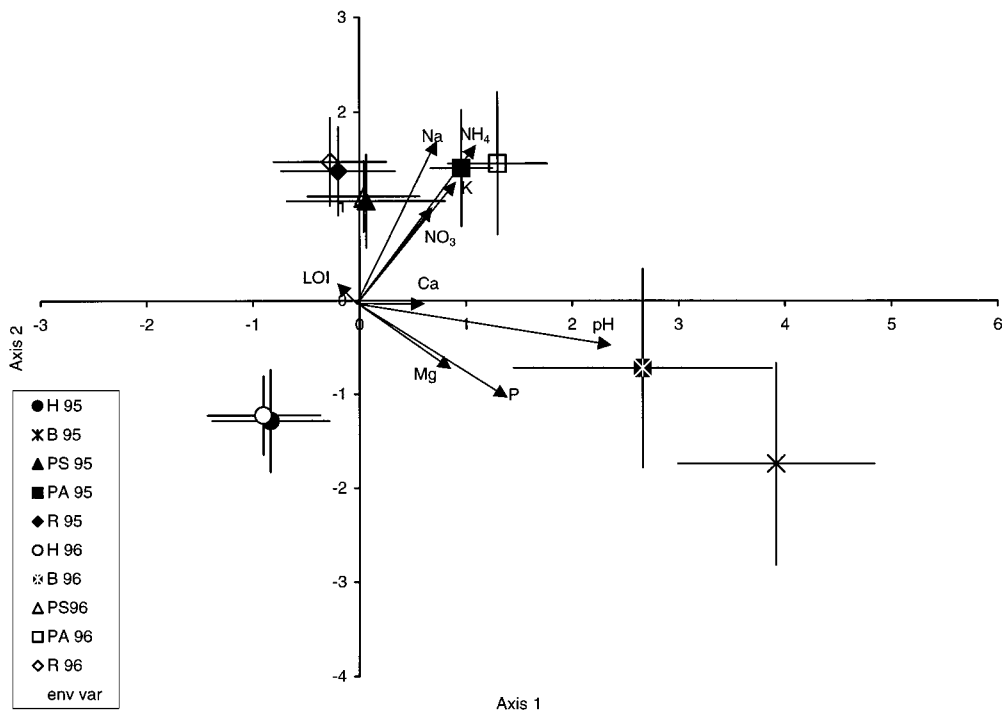
**Fig. 5.** Ordination diagram from CANOCO for the first two axes showing the relationship between the different successional stages and the soil nutrients on the Dorset Heaths. The soil nutrient vectors are shown by arrows. Heath, open heathland; B, *Betula* spp. is the major invader; PS, *Pinus sylvestris* is the major invader; PA, *Pteridium aquilinum* is the major invader; and R, *Rhododendron ponticum* is the major invader. Ca, exchangeable calcium; K, exchangeable potassium; LOI, percentage loss on ignition; Mg, exchangeable magnesium; Na, exchangeable sodium;  $\text{NH}_4$ , extractable ammonium-N;  $\text{NO}_3$ , extractable nitrate/nitrite-N; and P, extractable phosphorus.

- (1) There were many different successional trajectories along which a heathland may move, the different successional trajectories being characterised by the major dominant successional species.
- (2) Different soil nutrients increased with different successional trajectories; P, Ca and pH with *Betula*, nitrogen (ammonium and nitrate/nitrite) with *Pteridium aquilinum*, Na with *Rhododendron ponticum* and organic matter (loss on ignition) with *Pinus sylvestris*.
- (3) Some successional stages (*Pinus sylvestris*) were shown to be closer to the heath and to have undergone fewer successional changes in terms of both the vegetation and the soil nutrients than others (*Betula*). It was suggested that those stages closer to the heath in the ordination diagram would be easier to restore to heathland than those

stages further away. Stages listed in order of closeness to heath were *Pinus*, *Pteridium*, *Rhododendron* and *Betula*.

### Testing the repeatability

Those sites surveyed in both years were first analysed to test whether any drift had occurred through time (Fig. 6). Little change occurred in any of the successions except for the *Betula* site. It is perhaps to be expected that little change occurs as the samples were taken only one year apart, but the correspondence between the data implies that the approach is repeatable. The change in the *Betula* site may be due to insufficient replication (only one site was comparable between years) or because of the other factors such as the drought in the summer of the first survey. Long-term monitoring is needed to as-



**Fig. 6.** Ordination diagram from CANOCO for sites sampled in both 1995 and 1996. The 1996 sites were put into the 1995 model as passive samples and the figure shows the movement of the sites between years. The symbols are centroids for the sites and the lines are standard deviations, the soil nutrient vectors are shown by arrows. H, open heathland; B, *Betula* spp. is the major invader; PS, *Pinus sylvestris* is the major invader; PA, *Pteridium aquilinum* is the major invader; and R, *Rhododendron ponticum* is the major invader. Ca, exchangeable calcium; K, exchangeable potassium; LOI, percentage loss on ignition; Mg, exchangeable magnesium; Na, exchangeable sodium; NH<sub>4</sub>, extractable ammonium-N; NO<sub>3</sub>, extractable nitrate/nitrite-N; and P, extractable phosphorus.

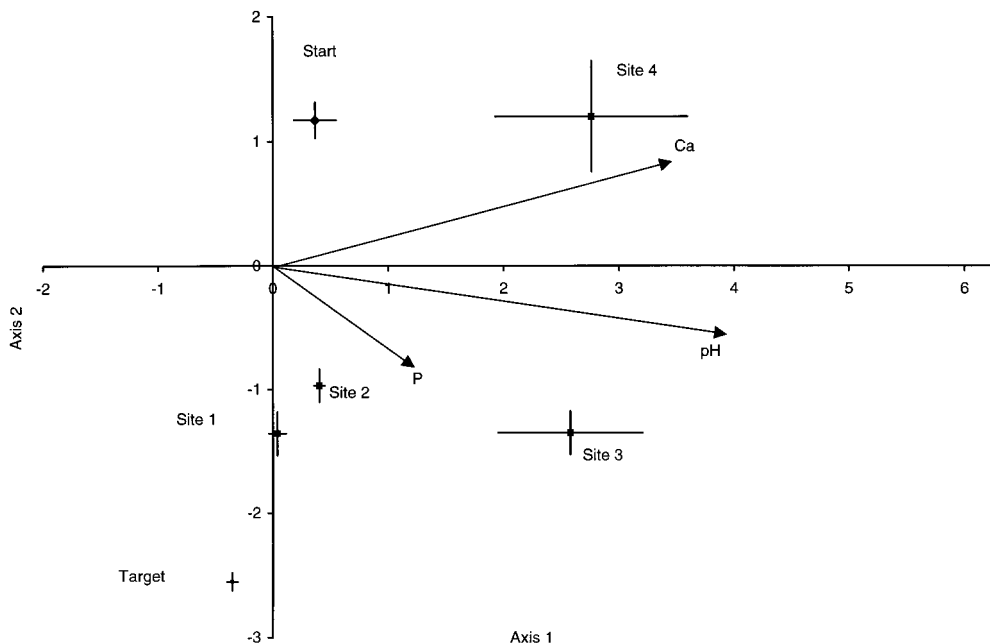
sess whether the late-successional sites are indeed at equilibrium and if not their rate of change.

### Effects of management

When the managed sites from the second survey were included in the analysis they were shown to fit into the model (Mitchell 1997). Figure 7 shows a simplified version of the results for the *Betula* sites. Of the four possible ways that a managed site could move (Fig. 3), the *Betula*-managed sites showed examples of three of these (Fig. 7). Managed site 1 has moved close to the heath ("target"), managed site 2 appears to be heading towards the heath but has not yet reached it, and managed sites 3 and 4 appear to be heading in different directions altogether. It was possible to plot similar diagrams for each of the other successional stages and their corresponding managed sites (Mitchell *et al.* 1999). These diagrams allowed us to see which sites were "successfully" managed, which sites were heading in

an undesirable direction and which may need additional management to restore them to heathland. The distance of the managed site from the heath and the late-successional communities can be calculated in multi-dimensional space using the Euclidean distance (Manly 1986); this uses Pythagoras' theorem in "n" dimensions to calculate the distance between two points. As there are nine environmental variables and therefore nine axes, the distances could theoretically be calculated in nine dimensions. However, as over 80% of the explained species-environment relationship was explained by the first four axes, the calculations were confined to four dimensions. The distance of the heath to managed sites provides a direct measure of the management success. An example of this is given in Table 5 for the managed *Betula* sites.

A measure of how straight the trajectory ( $A$ ) is between late-successional communities, managed and heath sites can also be made. For a straight line a value of zero should occur where  $A = (T + S) - D$ , and  $T$  is the distance from managed site to the



**Fig. 7.** CANOCO diagram to show the movement of managed *Betula* sites (sites 1, 2, 3, 4) from the late-successional site. The symbols represent centroids of the managed, late-successional (Start) and heath (Target) sites and the lines are standard error bars. Increasing leaves of exchangeable calcium (Ca), extractable phosphorus (P) and pH are shown by the arrows. Reproduced from *Journal of Applied Ecology*, 36, 770–783.

**Table 5.** Distances in four dimensions of managed-*Betula*, heath and *Betula*-successional sites from each other (reproduced from *Journal of Applied Ecology*, 36, 770–783). The *A*-value gives a measure of whether the managed site is on a straight line trajectory from the successional to the heath site { $A = \text{distance from managed site to heath } (T) + \text{distance from managed site to successional sites } (S) - \text{distance from successional site to the heath site } (D)$ }. The closer this value is to zero the closer the trajectory is to a straight line.

Site	Distance of managed site from		Distance of successional site from heath <sup>D</sup>	<i>A</i> -value
	Heath <sup>T</sup>	Successional site <sup>S</sup>		
Site 1	1.09	3.82	4.82	0.09
Site 2	2.56	1.96	4.22	0.30
Site 3	7.88	4.42	7.49	4.81
Site 4	7.15	4.65	5.57	6.23

heath, *S* is the distance from the managed site to the late-successional communities, and *D* is the distance from the late-successional communities to the heath. If the trajectory is a straight line then the managed site is moving directly towards the heath. However, if *A* is large then the trajectory is not straight and the managed site is moving in a different direction. In our data sites 3 and 4 have high *A*-values (Table 5) and are moving in a direction other than towards the heath (Fig. 6).

For simplicity we have assumed that the trajectories are linear, but it is possible that many trajectories will be curvilinear, and where this occurs the implications must be accommodated in the management of the site. However, the use of our approach allows the manager to detect this relationship and make a judgement as to whether it is acceptable for conservation purposes, or whether other management must be applied to correct the direction of change.

#### Measuring resilience

The distance between the late-successional community and the managed site (Table 5) is a combined measure of the force of management and the resilience of the late-successional communities. Site 1 may be close to the heath because it had a high level of management force applied to it or because of the low resilience of the site or both. Site 2 may be further away from the heath than site 1 because it has a higher resilience. However, a true measurement of resilience cannot be made until the sites are re-surveyed and the rate of movement of the ecosystem towards the heathland measured. We were unable to do this from the current data avail-

able, but suggest that perhaps an interval of at least five years is needed for change to become detectable. However, we have shown the potential of this method to measure resilience rates in heathland using vegetation and soil data, and we believe that other organisms could be included in the future, for example invertebrates and soil micro-organisms.

#### Discussion

In restoration ecology the main paradigms used to develop management policies are that there is either stability within the ecosystem/community (*nature-in-balance paradigm*) or that patterns of ecosystem changes are influenced by its past (*nature-in-flux paradigm*) (Urbanska 2000). Most conservation practice, restoration work and theories of ecosystem stability are based on the nature-in-balance paradigm, which implies an acceptance that there are stable successional end points, after which processes are in dynamic equilibrium (Parker & Pickett 1997). It suggests that any unit of nature is in and of itself conservable, and that the systems within that unit will maintain themselves in balanced equilibrium (Pickett *et al.* 1992). Thus, systems that are conserved and isolated from direct human perturbation will maintain themselves in the desired state for which they were originally conserved. Furthermore, systems disturbed from equilibrium will return to that same equilibrium (Pickett *et al.* 1992). The nature-in-flux paradigm suggests that this is an oversimplification and there are many states for a natural system to have and many ways to arrive at those states (Pickett *et al.* 1992). It assumes that ecosystems are open, can be reg-



ulated by external processes, and are subject to natural disturbances. The system may have multiple and probabilistic successions, which at some scales may lead to multiple equilibria, while at other scales may fail to reach an equilibrium. Because systems are open to external regulation, including human influence, these factors must be incorporated in ecological models for restoration ecology to be effective (Parker & Pickett 1997). Parker & Pickett (1997) argue that the nature-in-flux paradigm is the only valid approach for restoration work. The nature-in-balance paradigm aims to preserve or re-establish groups of species or habitats, the nature-in-flux paradigm aims to maintain the processes that have generated the desired habitat or group of species.

Current conservation work is often based on the nature-in-balance paradigm where the aim is to conserve a particular habitat or group of species. Restoration work is often targeted at restoring a particular community. As discussed earlier this concentration on particular groups or habitats within the UK is largely because many of the UK's endangered habitats are in small and isolated areas. There is, therefore, a desire to minimise the scale of the fluxes occurring within the system because of the fear that certain species may not survive if the change is too great. However, fluxes clearly do operate in natural systems, be they successional changes (autogenic or allogenic change), natural or changes caused by humans. Ecosystems are not static, yet conservation managers need to be able to maintain a system at quasi-equilibrium. To do this they need a method to measure how stable the system is and how quickly the system is changing. They must be able to measure many variables at one time and to have an objective scale by which to measure ecosystem change. We believe the approach outlined here could help to achieve these aims. The model can be used for assessing perturbations and the resulting impacts in conservation biology, enabling conservation managers to answer the questions posed at the beginning of this paper. While the example here showed data collected only one year apart, measurements of ecosystem resilience based on properties of both ecosystem structure and function could be calculated if data were collected over a longer time period. Data from such a sequence would also en-

able clearer answers to questions about the stability of managed sites and how quickly they may change between states.

As well as assessing the stability of a system, the model can be used to measure the impact of human activities on a system. In particular, it allows conservation managers to measure the success of conservation management work to restore habitats, by measuring movement towards or away from two "fixed" points, starting and target habitats. However, the model also allows the movement of these "fixed" points to be measured. It enables the efficacy of different management methods to be assessed with respect to the success of achieving the correct trajectory, and identifies those management techniques that result in different trajectories. It provides information that helps prioritise action (i.e. which successional stages are easiest to restore to heathland). Repeated measurements allows progress to be monitored and detects when a community is moving in the wrong direction after management, i.e. a community other than the desired one is establishing. With greater insight into these successional trajectories we may be able to apply additional management to "problem sites" that will subtly correct or fine-tune the direction of change, encouraging the target community to establish.

The model can measure the variability within the ecosystem under investigation and can identify which environmental variables are likely to be the most important driving variables in the ecosystem. This can be done at a variety of scales. Our studies on the Dorset heaths covered the lowland heath biotope at the individual site and regional scale. Goddard (1999) has compared two regions successfully, and there is no reason to suppose that a model could not be developed to cover all regions in the UK or even Europe. Other plagio-climax biotopes with high conservation interest such as reedbeds and grassland communities could also be studied using the same method.

This model, unlike other models, does not give information on the processes involved, i.e. why some ecosystems are more resilient than others, or how species richness relates to resilience, nor does it provide mathematical formula to predict ecosystem resilience. It merely measures direction and change through time against internally-derived standards. However, the model provides a more

complete picture of ecosystem resilience than simple measures based on species abundance as it combines measurements of both ecosystem structure and function, and can include biotic and abiotic components. Use of such multivariate models can highlight important hypotheses that may be tested by further experiments, and puts conservation experiments on a sound theoretical footing.

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