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MODELLING VEGETATION SUCCESSION IN ABANDONED ARABLE FIELDS IN BRITAIN[1]

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Abstract. Under the 'Set-aside' scheme of the European Community, many British fields that were formerly arable have been withdrawn from agricultural use. Resulting vegetation changes are hard to predict from past experience, because the arable weed flora is now very much smaller than when the classical studies of old-field succession were made.

In an attempt to predict changes that will occur in these fields, a computer model called SETSARIO has been written. In this model, both the seasonal dynamics of species and the management of the field are taken into account. The model starts from an initial floristic composition, including information on species present in the seed bank. The initial composition is represented merely by the order of magnitude of species abundance, more precise values being thought to be rather unimportant in determining the outcome as well as hard to obtain in practice. Subsequent changes are represented by a projection matrix from one season to the next.

Competition between species at any one season is represented by a hierarchy of bids for space. Annuals lose their early dominance because at certain seasons they disappear, and therefore lose control of space. It is difficult for them to regain space once it is lost. The model has no explicit representation of spatial dynamics, but clonally spreading species such as *Elymus repens* are able to spread more effectively in the face of competition from existing vegetation than are species that reproduce only from seed.

Management of the field is by mowing or tilling. This is represented by altering the values of transfer probabilities between seasons. Allowance is made for the size of species, with tall plants being more affected by cutting than short ones.

The model occupies a position intermediate between a detailed population model and one which merely describes vegetation change. The merits of modelling at this level of resolution are discussed.

Introduction

The 'Set-aside' scheme of the European Community is a voluntary scheme designed to reduce surpluses of arable crops. In Britain it is administered by the UK agriculture departments. First registrations were in autumn 1988. Farms registering at that time took arable fields or parts of arable fields out of production for a period of at least 3 years starting 1989.

The main option of the Set-aside scheme is 'permanent fallow', whereby land must be cut at least once a year and not sprayed with agricultural chemicals. Grazing by horses is permitted but not by cattle or sheep. If the farmer wishes, he may sow a cover crop, and he may cultivate the soil in winter. In practice, most farmers entering the scheme have allowed their fields to revegetate naturally and have contented themselves with a once- or twice-yearly cut.

There has been widespread interest in the possibility of using Set-aside not merely to reduce agricultural production but also to improve the environment. For this purpose, the potential results of applying various management treatments are of interest. In particular the possibility of a non-intervention treatment, with no annual cut, can be considered. There is also the possibility of sowing various plant species which may have a beneficial effect either on game and other wildlife or by improving the appearance of the countryside.

Predicting the course of succession

The course of succession depends on the climate, the soil, the management regime and the initial floristic composition (Egler, 1954). Given these conditions, and given a comparable succession described from the past, ecologists should be able to predict what will happen during successions under Set-aside.

In Britain, the classic observations of succession on abandoned arable land were made at Rothamsted, in the Broadbalk Wilderness experiment (Brenchley and Adam, 1915; Tansley, 1939). Broadbalk is on a clay loam with about 3% calcium free calcium carbonate; prior to abandonment it had been in cultivation for a

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long time, possibly since Roman times (Jenkinson, 1970). From 1843 to 1882 it was unmanured and was cultivated annually for wheat. In 1882 the wheat crop was not harvested and was allowed to seed itself.

Many species took part in the subsequent succession. After 4 years, the clonally spreading *Agrostis stolonifera* (nomenclature follows Dony *et al.* (1986)) was dominant, together with large quantities of the annual legume *Medicago lupulina*; many other clonally spreading species were prominent in the community. Much the same species prevailed in year 13, except that *M. lupulina* had been replaced by the perennial legume *Lathyrus pratensis*. After about 20 years, the tussock-forming grass *Dactylis glomerata* had become dominant.

To a modern ecologist, a remarkable feature of the Broadbalk succession is the wealth of species available to colonize from the weed flora. Indeed, only one important species, *Arrhenatherum elatius* was completely absent from the initial weed flora. It took 20 years to become abundant, and, in part of the experimental area from which woody vegetation was cleared, eventually became dominant after 30 years.

Initial floristic composition

In autumn 1989, several fields that had been abandoned from agriculture for 1-5 years were examined in southern England. It was clear that modern successions are remarkably different from that seen on Broadbalk. In fields that had been in continuous arable cultivation from more than about 7 years, few perennial species had survived. Often there were patches of *Cirsium arvense*, *Elymus repens*, together with scattered *Convolvulus arvensis*. But these were generally in very low abundance and completely absent from most of the area.

It was also clear that few species had spread into the field from the edge. The chief invaders were *Crepis vesicaria*, *Epilobium* spp. and *Taraxacum officinale*, all plants with wind-dispersed seeds. Thus, for the purposes of predicting succession, it is reasonable to assume that the initial floristic composition (in autumn following the last harvest) consists of those species that are present as rooted individuals or as seeds (including the seed bank), together with wind-blown seeds of colonists from the edge.

Given such an initial composition (see, for example Table 2 below), the course of succession cannot readily be predicted by analogy with old-field successions from the past. A modelling approach to the problem is required.

A computer model of the successional process

A FORTRAN program called SETSARIO (SET-aside ScenARIO) has been written to predict succession from a given initial floristic composition. The program has been written specifically for the management prescriptions allowed under the Set-aside Scheme. These include cultivation, mowing and grazing. Set-aside fields must be mown at least once a year. Thus woody vegetation, which might become dominant if the field were not mown, is not represented. Climate and soil are also not specifically represented.

Time

Time is represented discretely by years divided into 4 seasons, and there is an option in the model to step slowly through the seasons to examine the state of the system in detail as it changes. The seasons are:

1. Winter (January 1)
2. Spring (April 1)
3. Summer (July 1)
4. Autumn (October 1).

The dates are only approximate, but the model depends crucially on seasonal dynamics. In particular, annuals die back in autumn and make space that may be occupied by perennials or by the next generation of annuals.

State variables

The state of the field at any time is represented by variables specifying (1) the condition of the site and (2) the abundance of species in various life-stages. These variables represent the state of a moderate-sized area, perhaps a 10-m square, but the area is not specified explicitly, so that the model can, with reduced realism, be used to represent the state of a whole field.

The condition of the site is represented by 4 variables:

1. Thick vegetation
2. Thin vegetation
3. Litter (including straw)
4. Bare ground.

These variables are effectively only 3 variables, because they must sum to 100% cover of the ground. No seeds can germinate in thick vegetation, few in thin vegetation or litter. The number of seeds that can germinate on ground in either of these states depends on the gap-requirements of the individual species represented.

The state of each species is represented by 5 life stages:

1. Seed
2. Seed bank
3. First-year (young) cohort
4. 2nd and later-year 'cohort' (non-dormant)
5. Dormant plants (hidden).

In winter, some species such as *Convolvulus arvensis* are completely in the dormant and seed states (states 1, 2 and 5). Likewise, in the autumn, *Anthriscus sylvestris* is dormant.

Growth and germination

Growth is represented by an increase in the quantity of vegetation from one season to the next, and germination by a transition from the seed stage to the vegetative stage. Both are limited by the amount of space available, which is allocated in accordance with a hierarchy of claims on space. Established plants automatically claim the space they occupy, as do dormant (life-stage 5) perennials, which claim their space as established plants. Claims on space are never satisfied in full; instead, if a total claim c exists for space s, then y, the amount of space occupied, is given by

$$y = s\,(1 - e^{-c/s}).$$

The rationale for this method of space occupation is that y is the amount of space that would be occupied if the claim were composed of randomly placed individual plants or ramets, each of which is assigned independently to part of the area in the space. Specifically, if each fragment of the space is the same size as an individual (or ramet), then the chance that it is unoccupied is

$$e^{-c/s}$$

the first term of a Poisson distribution (*cf.* Greig-Smith, 1983, p.13). Note that even when the space claimed c is bigger than the space available s, some space is unoccupied.

Each of the hierarchical claims on space is called a 'bid', and there are 4 bids in all:

Bid 1: Claims by plants for that vegetation space that is already occupied; this forms thick vegetation.

Bid 2: Claims by plants for space in the area adjoining that which is already occupied.

Bid 3: Claims by plants for less accessible space, further away from existing vegetation, and available to clonally spreading plants or those returning from the dormant state.

Bid 4: Claims by seedlings for space; no seedlings can establish in thick vegetation, some seedlings (depending on species) can establish in up to 20% of the thin vegetation and in 10% of the litter space.

In Bid 2, the area available for colonization is at most twice the area of existing vegetation, so that vegetative growth cannot increase the amount of a species by more than 9-fold over two seasons.

Death and hiding of vegetation

Death of plant material generates litter. Death of unit area of thick vegetation generates unit area of litter; thin vegetation generates only half as much litter. Litter disappears (rots and is comminuted) quite rapidly, 30% decaying from one season to the next.

Litter is also generated when plants go into the dormant state. No plant hides for more than one season, and when a dormant plant emerges, it immediately claims (but may well not be awarded) twice the space that it had before it died back.

If a plant does not become completely dormant at any season, it dies back partially in the winter, with the amount of die-back being transferred to the dormant state. Partially evergreen species undergo a 50% die-back; totally evergreen species undergo a 20% die-back.

Seed production

Seed production by annuals is represented as a 20-fold increase; this means that enough seed is produced to occupy 20 times the area that was occupied by the seed parents. Perennials can only achieve a 10-fold increase in this way. Most perennials do not produce seed in the first year, but *Epilobium* spp. and non-vegetatively spreading grasses do produce seed in the first year.

Transitions between life stages

The crux of the model is a matrix of coefficients, specifying the magnitude of transitions between life stages (Table 1). In addition, there are two extra coefficients specifying how much litter a plant will generate by dying or becoming dormant.

Table 1. Projection matrix for transfers between life stages; columns refer to the stage at time t, rows to the stage at time t+1.

Life stage	1	2	3	4	5
1 Seed	a_{11}	a_{12}	a_{13}	a_{14}	-
2 Seed bank	a_{21}	a_{22}	-	-	-
3 1st year plant	a_{31}	-	a_{33}	-	-
4 Older plant	-	-	a_{43}	a_{44}	a_{45}
5 Dormant plant	-	-	a_{53}	a_{54}	-

The coefficients for litter production do not depend on the season or on the species of plant. The other coefficients mostly depend on both. They are designed to reflect the seasonal dynamics and individuality of the species.

It would be tedious to explain here how each coefficient is calculated. Two examples should suffice. The coefficient a_{22} specifies the persistence of seeds in the seed bank from one season to the next. The species are categorized into 4 seed-bank types according to the scheme of Grime *et al.* (1988):

1. No seed bank; seeds germinate almost at once
2. Most seed persists only till the next growing season
3. Seeds persist in the soil, but have a low abundance
4. There is a large bank of persistent seeds through the year.

Rules governing the seed-bank coefficient a_{22} are then as as follows:

Type 1. $a_{22}=0$ Seeds never enter seed bank

Type 2. $a_{22}=0.2$ 80% of seeds die from one season to the next

Type 3. $a_{22}=0.95$ 5% of seeds die from one season to the next

Type 4. $a_{22}=0.99$ 1% of seeds die from one season to the next.

The effect of a cultivation is to kill a further 40% of the seeds in the seed bank; *i.e.* for a season in which there is cultivation, a_{22} is reduced by 40% from its normal value. In the absence of cultivation, Type 3 seeds survive on average for 5 years, and type 4 seeds for 25 years.

As another example, consider a_{43}, which specifies the transition from life stage 3 (first-year plants) to life stage 4 (secondyear-and-older plants). This transfer is zero except at the end of the year, *i.e.* it is only nonzero for the transition from Season 4 (autumn) to Season 1 (winter). It is zero for annuals, which die, and zero for those parts of the plant that transfer to the dormant state.

In effect, for perennials in autumn,

$a_{43} = 1 - a_{53}$

The value of the coefficient a_{53} depends on the leaf phenology of the species. Phenology categories are those recognized by Grime *et al.* (1988) and are seasonal-aestival (duration of canopy spring to autumn), seasonal-hibernal (duration of canopy autumn to early summer), evergreen-always, and evergreen-partial (leaves slowly but incompletely senescing over winter). The magnitude of the transfer to dormant parts of the plant is then given by:

Seasonal-aestival $a_{53}=1$ These plants become dormant

Seasonal-hibernal $a_{53}=0$ Plants come out of dormancy

Evergreen-always $a_{53}= 0.2$ Slight winter die-back

Evergreen-partial $a_{53}=0.5$ Moderate die-back.

Clonally spreading plants such as *Elymus repens* are deemed to be only partially evergreen, even if they are classified by Grime *et al.* (1988) as wholly evergreen.

Competition between species

Competition between species is represented by their bids for space. They make claims for available space and being allotted a proportion of their claim. For example, if the field is 50% bare and the bare ground is claimed by two annuals, A1 bidding for space 3.0 and A2 bidding for space 6.0, then the total space occupied will be 0.5 $(1\text{-}e^{-18})$, which is effectively all the bare ground. The occupied ground is allocated to species in proportion to the size of the claim; thus A1 will get one-third and A2 two-thirds.

Succession within the perennial life-form is represented by giving species that are thought to be superior competitors a slightly higher (5% per season) growth rate. In the absence of mowing, species classified by Grime *et al.* (1988) as competitors (*i.e.* having the C, C-R and C/C-S-R strategies) have a slightly higher (5% per season) growth rate.

In its present form, the model also includes an element of 'knowing the answer'. Thus, if the managment is by grazing, then species known to be common in pastures have their growth rate increased by 5%. If the vegetation is mown in July, then species known to be characteristic of hay meadows have their growth rate increased by 5%. If the ground is cultivated, then species known to be arable weeds have their growth rate increased by 5%.

All features previously described are additive. That is to say, if species S is arbitrarily divided into subspecies S1 and S2 with the same attributes as S, then model behaviour will be the same as if it is run with species S undivided. One major nonadditive feature is, however, included. The effect of this is to reduce the growth rate of a highly abundant species in spring or summer, especially if that species is not one which would not be expected on a roadside. The purpose of this non-additivity is to reduce the tendency for a single species to become overwhelmingly dominant.

Results

Initial conditions for a run of SETSARIO are shown in Tables 2 and 3. The program also requires initial conditions for the site. These were entered as 1% thin vegetation, 30% litter (by presumption this is cereal crop straw) and 69% bare ground. Note that initial species abundance is entered only as orders of magnitude. Each individual plant is reckoned to be about 0.01 m^2 in area, so that an initial cover of 0.001% (the lowest value entered) corresponds to a density of about 10 plants/ha.

The resulting scenario (Table 4; Fig. 1) shows a pattern of compositional change very comparable to that found by Brown & Southwood (1987) at another site in England. Annuals dominate for the first two seasons; perennials exceed them in year 3 and eliminate them almost completely by year 6. Of the perennials, by far the most important is *Poa trivialis*, which initially is an almost insignificant component, with 0.01% cover, *i.e.* about one plant per 100 m^2. However, it increases exponentially by a factor of 10 for each of the first 3 years, reaching a peak of abundance in year 7. *Lolium perenne* starts from an even lower density and only begins to achieve prominence towards the end of the succession.

With such an intense cutting regime, the taller perennials such as *Cirsium arvense*, *Epilobium hirsutum* and *Senecio jacobaea* are kept well in check. However,

Table 2. Initial state of system for a run of SETSARIO, based ona Set-aside field near Cambridge, England, autumn 1989.

Species	Seed	Seed bank	1-year plants	Older plants	Dormant plants
(a) Annuals					
Alopecurus myosuroides	10.00	-	-	-	-
Bromus commutatus	10.00	-	-	-	-
Hordeum vulgare	10.00	-	-	-	-
Senecio vulgaris	.10	-	-	-	-
Sinapis arvensis	.01	-	-	-	-
Sonchus asper	.10	-	-	-	-
Veronica persica	.01	-	-	-	-
(b) Biennials					
Cirsium vulgare	-	-	.01	-	-
Picris echioides	-	-	.01	-	-
(c) Perennial herbs					
Cirsium arvense	-	-	-	.10	-
Convolvulus arvensis	-	-	-	1.00	-
Epilobium hirsutum	-	-	-	.01	-
E. tetragonum	-	-	-	.01	-
Senecio jacobaea	-	-	-	.01	-
Taraxacum officinale	-	-	-	.01	-
(d) Perennial grasses					
Lolium perenne	-	-	-	-	-
Poa trivialis	-	-	-	.01	-

Table 3. Management parameters for a run of SETSARIO

Parameter	Value
Cut in May; leave cuttings	1
Cut in July; harvest hay	0
Cut in July; leave cuttings	1
Cut in Sept; leave cuttings	1
Graze all year	0
Graze aftermath of hay cut	0
Light cultivation in March	0

Convolvulus arvensis is able to increase in the early years.

In the early years, the winter vegetation (Fig. 1b) contains rather a large amount of plant litter, resulting from death of annuals and *Convolvulus arvensis*. The seed bank (not shown here) eventually is dominated by *Poa trivialis*, with a lesser quantity of *Veronica persica*. The annual grasses do not have a persistent seed bank, and are known to germinate or die within about 2 years (Roebuck 1987).

Discussion

A model such as SETSARIO with 26 attributes recorded for each of 132 species must inevitably have rather a complex structure which is not readily tested by varying the parameters. It purports to predict the actual change in species composition at a site, and in this sense is comparable to the models of forest succession discussed by Botkin *et al.* (1972) and Shugart *et al.* (1988). These models all employ large numbers of parameters, not all of which can be measured accurately. They usually also include some unrealistic assumptions, designed to achieve a known answer. For example, the model of Botkin *et al.* (1972) included multiplicative factors to ensure that species had zero growth at their climatic extremes.

Shugart *et al.* (1988) observe that most succession models have been developed for forested systems. This was partly due a simultaneous and relatively independent interest in modelling forest dynamics that developed in forestry and ecology in the early 1970s. It is also because trees occur mostly as discrete individuals and can therefore be enumerated and measured throughout their lives. Spatially explicit models can be calibrated and tested.

In much herbaceous vegetation, including weed communities and reverting arable fields, many of the most important species spread clonally and do not have discrete individuals except at the level of the individual shoot. Moreover, the influence of short-term factors such as weather or insect outbreaks will be greater. In all successions involving colonization, there is also a large element of chance, depending on the proximity of nearby seed sources (Glen-Lewin 1980; Gill and Marks 1991).

Can a model at the spatial scale of SETSARIO be useful? The model notionally describes quite a small area, perhaps 100 m^2. If there are non-uniformities at a larger scale, then units could be fitted together as cells

Table 4. Cover % of species predicted by SETSARIO in summer, given initial conditions specified in Tables 2-3.

Species	Year									
	1	2	3	4	5	6	7	8	9	10
(a) Annuals										
Alopecurus myosuroides	16.1	17.9	8.7	2.3	.1	-	-	-	-	-
Bromus commutatus	20.6	29.9	19.7	7.7	.8	-	-	-	-	-
Hordeum vulgare	17.2	17.5	8.0	2.2	.2	-	-	-	-	-
Senecio vulgaris	.3	.3	.1	-	-	-	-	-	-	-
Sinapis arvensis	-	-	-	-	-	-	-	-	-	-
Sonchus asper	.3	-	-	-	-	-	-	-	-	-
Veronica persica	.1	.5	1.6	3.3	1.9	.4	.1	-	-	-
(b) Biennials										
Cirsium vulgare	.1	.1	-	-	-	-	-	-	-	-
Picris echioides	.1	.1	.2	.1	.1	-	-	-	-	-
(c) Perennial herbs										
Cirsium arvense	.7	2.6	5.4	6.3	5.1	3.9	3.0	2.3	1.7	1.3
Convolvulus arvensis	6.6	21.5	35.6	30.6	19.7	12.5	8.4	5.8	4.0	2.8
Epilobium hirsutum	.1	.4	.9	1.4	1.4	1.3	1.3	1.2	1.1	1.0
E. tetragonum	.1	.4	1.1	1.7	1.9	1.9	1.9	1.9	1.8	1.7
Senecio jacobaea	.1	.4	1.1	1.7	1.9	2.0	2.0	1.9	1.9	1.8
Taraxacum officinale	.1	.6	2.4	4.9	6.9	8.5	10.1	11.6	12.9	13.8
(d) Perennial grasses										
Lolium perenne	-	.1	.4	1.2	2.2	3.3	5.0	7.2	9.9	13.1
Poa trivialis	.1	1.5	9.6	33.8	56.5	65.3	67.8	67.7	66.2	64.1

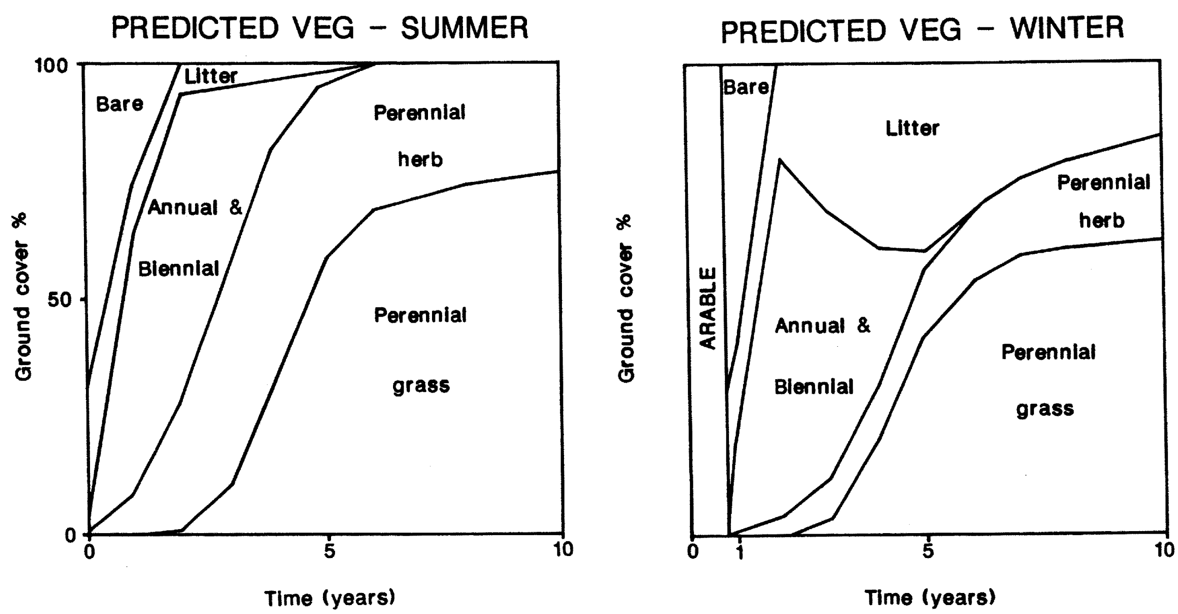

Figure 1. Ground cover % predicted by SETSARIO in (a) summer and (b) winter, given the initial conditions in Table 2 and the management parameters in Table 3. For the purposes of illustration, plant species have been grouped into categories; corresponding cover values for individual species in summer are given in Table 4.

on a spatial grid, with rules for species dispersal between the cells. This would not be impossibly demanding of computer time; SETSARIO was written on a desktop computer (IBM PC 'clone'), on which it takes only a few seconds to model the passage of 10 years.

The original purpose of SETSARIO was to clarify the likely course of succession when the initial floristic composition was lacking most mid- and late-successional species. Statements based on past experience would be false because particular functional types of species would be absent. Its purpose was to express an explicit view of the way succession operates. Another possibility would have been to set up rules for succession, in the form of an expert system (Noble 1987). This route was not followed, because rules are generalizations and would apply better to functional types than individual species.

Perhaps the greatest value of the model has been in focussing attention on the question of what information is necessary to make useful predictions of succession. In the example considered above, it was predicted that *Poa trivialis* would become dominant in year 5 and would delay the spread of *Lolium perenne*. In fact, *P. trivialis* might not be so effective a delaying influence, because in dry summers it dies back to a state approximating summer dormancy. This would leave gaps that could readily then be colonized by *L. perenne*.

The gaps might also result in longer-term persistence of the annuals. A theoretical study (Crawley and May 1987) has shown an annual with no competitive ability can persist if sufficient gaps become available; and some of the annuals in the example, particularly *Bromus commutatus*, have considerable competitive ability.

With forest models there has been a shift away from the initial emphasis on forecasting patterns of change towards the more theoretical focus of understanding the scaled-up consequences of various theoretical and ecological processes (Shugart *et al.*, 1988). A model like SETSARIO can readily be developed by building in a more realistic representation both of canopy architecture and of the relation between species performance and environmental factors such as soil moisture and fertility. This is the problem that now needs to be addressed if ecosystem function and species composition are to be linked.

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