PLANTWORLD:
Population Dynamics in Contrasting Environments

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Abstract

PLANTWORLD was developed to examine the effects of including evolvable phenotypic behaviour in ecological models and the resultant population dynamics in contrasting (stable vs. disturbed) environments. It also demonstrates some interesting and biologically plausible feedbacks between population attributes and evolutionary dynamics. PLANTWORLD represents a state-of-the-art A-Life system for integrating evolutionary and ecological dynamics. Its highly efficient design and implementation is able to support over half a million agents (PLANTS) on a standard PC, that evolve and behave according to their experience of different environments.

1 INTRODUCTION

Numerical ecological models predict that in stable environments populations will exhibit logistic growth to *carrying capacity* and thereafter, exhibit only small fluctuations around the equilibrium value (Lotka 1924). In more variable or disturbed environments populations will frequently be set back to lower values and re-growth will lag behind increasing resources. Populations in these environments should exhibit strong fluctuations, rarely reaching or remaining at equilibrium. Hence, population dynamics should reflect the variability inherent in the environmental regime. Many predictions regarding organismic and community attributes, as well as population-level attributes, follow from these dynamics (MacArthur and Wilson, 1967; Odum, 1971; May, 1973; Wiens, 1984). Some of these are listed in Table 1. More recent models show that spatial dynamics can mitigate instabilities arising from high stochasticity (May 1973) and that more complex communities may persist in disturbed conditions without exhibiting asymptotic stability (Jansen 1987; Law and Morton, 1996). However, none of these models include phenotypic behaviour, particularly, they omit any *functional response* to resource variability or disturbance, which may mitigate the numerical response (mortality) at the population level. If this is the case, the attributes of organisms, populations and communities may not be strongly correlated with perceived levels of environmental variability as implied in Table 1. In this paper we report on experiments conducted in PLANTWORLD that show how a simple, evolvable functional response to environmental variability might affect population dynamics.

Table 1: Predicted organismic, population and community attributes in contrasting environments

STABLE	DISTURBED
Organisms	**Organisms**
K-selected	r-selected
Optimal Specialists	Opportunistic Generalists
Populations	**Populations**
Density dependence	Density independence
Niches saturated	Niches unsaturated
Communities	**Communities**
Saturated communities	Unsaturated communities
Biotic coupling	Biotic decoupling
High complexity	Low complexity

2 PLANTWORLD DESCRIPTION

PLANTWORLD consists of a 2-D grid upon which stationary agents (PLANTS) germinate from SEEDS, maintain themselves, grow, reproduce and die (Dyer, Bentley, & Shah, 2001). Each grid cell contains a single resource, *moisture*, that receives additional moisture from a rainfall timeseries each timestep. Moisture is removed from the grid by PLANTS, SEEDS and by evaporation. The PLANT's phenotypic behaviour is given by its underlying genome that determines its *AdultSize* (size at which it can begin reproduction, 1 - 2048) and its *dormancy strategy*. Its dormancy strategy determines its behaviour each timestep over an annual cycle. The possible monthly behaviours are:

kpon – the PLANT is unconditionally active and must acquire enough resources to meet maintenance requirements. Additional resources can be used for growth or reproduction.

kpoff – the PLANT is unconditionally dormant and does nothing except survive the timestep.

ks – the PLANT is conditionally active or dormant depending on whether available resources meet *maintenance requirements*.

The PLANT's dormancy genome therefore consists of an array of 12 symbols that determine its behaviour over twelve consecutive timesteps and is then repeated. For example, a PLANT with the following genome would be deterministically active for the first four timesteps (*kpon*), deterministically dormant for the next four timesteps (*kpoff*) and conditionally active/dormant for the last four timesteps (*ks*).

1	2	3	4	5	6	7	8	9	10	11	12
kpon	*kpon*	*kpon*	*kpon*	*kpoff*	*kpoff*	*kpoff*	*kpoff*	*ks*	*ks*	*ks*	*ks*

The alleles that allow dormant behaviour (*kpoff* and *ks*) incur costs in terms of *maintenance requirements* and these can be stipulated by the user. In the experiments reported here, these costs are set so that the conditional strategy (*ks*) incurs twice as much cost to maintenance as the unconditional strategy (*kpoff*). The PLANT's maintenance requirement is a function of its *CurrentSize* and its dormancy strategy according to:

$$m = (k_o + n_1\,[kpoff] + n_2\,[ks]\,) * CurrentSize$$

where

m = maintenance requirement
k_o = constant, set at 0.5 for these experiments
$[kpoff]$ = cost of each *kpoff* allele, set at 0.01 here
$[ks]$ = cost of each *ks* allele, set at 0.02 here
n_1 and n_2 = number of *kpoff* and *ks* alleles in genome
CurrentSize = the PLANT's current size (1 – 2048)

A PLANT germinates when its SEED acquires requisite moisture. In the next timestep, the PLANT's behaviour is determined by the leftmost allele in its dormancy strategy. If the PLANT is obligately dormant (*kpoff*) it does nothing. If it is obligately or conditionally active (*kpon* or *ks*) the PLANT checks out its available moisture. This is governed by the amount of moisture currently in the cell divided according to the number and biomass of other PLANTS in the cell. If the PLANT is in state *kpon* but cannot acquire enough moisture to meet *maintenance requirements*, it dies. If it is in state *ks* and cannot meet *maintenance requirements*, it goes dormant. If the PLANT can meet its *maintenance requirements*, it survives and uses any left over moisture for growth and reproduction.

The PLANT has a maximum rate of moisture utilisation that is a simple function of its *CurrentSize* (0.75 in these experiments). The PLANT's growth per timestep is given by the reciprocal of the square root of its *CurrentSize* (ensuring sub-exponential growth) multiplied by the resources left over after *maintenance requirements* have been met. The PLANT grows until it reaches its *AdultSize* at which point it can begin reproduction. The PLANT can reproduce in the subsequent timestep provided it is active, gains its *maintenance requirements* and another PLANT of similar *AdultSize* exists in its vicinity that also satisfies these conditions. When two PLANTS reproduce, they produce a number of SEEDS (stipulated by their *AdultSize*) that are distributed according to a random normal distribution on the landscape with certain standard deviation, from a centre occupied by one of the parents. SEEDS can remain dormant for a number of timesteps determined by their *AdultSize*. If the SEED does not germinate in this time-period, it dies. The moisture available for SEED germination is 10% of that left over after PLANTS have gained their maximum requirements. SEEDS to be germinated are chosen at random by the program, the number being determined by the amount of moisture available in the cell for germination. Each SEED requires a single unit of moisture in order to germinate. Once moisture has been used for germination, evaporation occurs, at a rate stipulated by the user. In the following experiments, the evaporation rate is set at 100%. Since no moisture is left in the cell at the end of each timestep, environmental variability is fully determined by the rainfall timeseries and the spatial distribution of receipts.

A further parameter influences PLANT behaviour. As the PLANT reaches certain *CurrentSize* thresholds it gains a *StorageEffect*. The *StorageEffect* determines the number of consecutive timesteps the PLANT can survive without being dormant or dying if *maintenance requirements* are not met. The first threshold kicks in when the PLANT reaches *CurrentSize* 200. In the following experiments, we only initialise experiments with PLANTS of *AdultSize* 129, so the *StorageEffect* does not affect PLANT behaviour in the following experiments.

PLANTWORLD's environment consists of a two-dimensional grid of cells called the *soil moisture grid*. Each cell contains moisture units. The size of the grid can be determined by the user and is set at 50 * 50 in the following experiments. Moisture reaches the grid via *rainfall*. The rainfall each timestep is given by timeseries data. This data can be artificial generated, but in order to include natural rainfall variability in the model, we also use real rainfall data. These data are monthly average rainfall gridded at 2.5° latitude by 3.75° longitude resolution at various locations around the globe over the years 1900-1999 (Hulme, 1999). Thus, with each timestep representing a single month, there are 1200 data points (100 years) in each timeseries. Since most experiments run for many thousand of timesteps, the timeseries used in each experiment is continuously re-cycled over the course of the run.

Each timestep, a spatial grid determine how much of the rainfall given by the timeseries is received by each cell on the *soil moisture grid*. Each cell on a spatial grid has a *Receipt Value* 0 – 15. The rainfall value given by the timeseries is scaled to the cell's *Receipt Value*, with *Receipt Value* = 0 implying no rainfall and a *Receipt Value* = 15 implying the value given by the timeseries. A different spatial grid can be called each timestep. Once the correct rainfall receipt has been calculated it is added to the amount remaining in the corresponding cell of the soil moisture grid (zero, if the *Evaporation Rate* is set at 100%). A single rainfall timeseries value can therefore be distributed fully homogeneously (same *Receipt Values* in all cells) or highly heterogeneously across the landscape.

3 EXPERIMENTS

Over 200 experiments have so far been conducted in PLANTWORLD. Here we report the results of a small selection of these that test the hypothesis: *that the evolution of behavioural responses to environmental variability will mitigate variability in population dynamics.*

In order to produce comparable results, the following experiments were carried out under standard initial conditions[1]. In all the following experiments we initiate PLANTWORLD with PLANTS of a single *AdultSize* (129)[2]. While different dormancy strategies are used to initiate different experiments, all PLANTS in each experiment are intitiated with the same dormancy strategy. Experiments are carried out in the following environments:

HH	fully homogenous landscape, constant rainfall receipts (artificial spatial and temporal data - 1000 units per timestep per cell)
HV	fully homogeneous landscape, naturally variable rainfall (real timeseries data)
HETV	heterogeneous landscape, naturally variable rainfall (real timeseries data)

The natural data used in the above experiments (HV and HETV) are average monthly values in millimetres for regions of the following countries:

UK	880
IRELAND	965
COLUMBIA	1216
ZIMBABWE	1025
BOTSWANA	593

The numbers on the right indicate the average monthly receipt in these environments over 100 years of data. All experiments 1 - 10 are initiated with 100,000 agents with 50:50 PLANT to SEED ratio.

Experiments 1 - 8 are initiated with 100% of the PLANTS carrying the following genome, referred to as the *full kpon* strategy:

1	2	3	4	5	6	7	8	9	10	11	12
kpon	*kpon*	*kpon*	*kpon*	*kpon*	*kpon*	*kpon*	*kpon*	*kpon*	*kpon*	*kpon*	*kpon*

Experiment 9 is initiated with 100% of the PLANTS carrying the following genome, which is referred to as the *mixed strategy*:

1	2	3	4	5	6	7	8	9	10	11	12
kpon	*kpoff*	*ks*	*kpon*	*kpoff*	*ks*	*kpon*	*kpoff*	*ks*	*kpon*	*kpoff*	*ks*

Experiment 10 is initiated with 100% of the PLANTS carrying the following genome, which is referred to as the *matched strategy:*

1	2	3	4	5	6	7	8	9	10	11	12
kpon	*kpon*	*ks*	*ks*	*kpoff*	*kpoff*	*kpoff*	*kpoff*	*ks*	*ks*	*kpon*	*kpon*

The following experiments were conducted:

Initiated with 100% full kpon strategy:		
1.	HH1000	homogeneous landscape, constant timeseries of 1000 units per cell per timestep
2.	HVUK880	homogeneous landscape, UK rainfall data (average 880 units per cell per timestep)
3.	HVIRE965	homogeneous landscape, IRELAND rainfall data (average 965 units per cell per timestep)
4.	HVCOL1216	homogeneous landscape, COLUMBIA rainfall data (average 1216 units per cell per timestep)
5.	HVZIM1025	homogeneous landscape, ZIMBABWE rainfall data (average 1025 units per cell per timestep)
6.	HVBOT593	homogeneous landscape, BOTSWANA rainfall data (average 593 units per cell per timestep)
7.	HETZIM1025	heterogeneous landscape, ZIMBABWE rainfall data (average 1025 units per cell per timestep)
8.	HETBOT593	heterogeneous landscape BOTSWANA rainfall data (average 593 units per cell per timestep)
Initiated with 100% mixed strategy:		
9.	HETZIM1025	heterogeneous landscape, ZIMBABWE rainfall data (average 1025 units per cell per timestep)
Initiated with 100% matched strategy:		
10.	HETBOT593	heterogeneous landscape, BOTSWANA rainfall data (average 593 units per cell per timestep)

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[1] There are many parameters in PLANTWORLD that can be set by the user. There is no room to list these here but they include such things as the initial number of agents and the ratio of PLANTS to SEEDS. Others, such as the dormancy costs, have been mentioned in the text.

[2] This AdultSize was chosen for two reasons. First, we want to neglect the StorageEffect for these experiments and second, population data is recorded according to CurrentSize categories, one of which is <= 128. Thus, by choosing an AdultSize of 129 we can determine the proportion of the current population that are adults.

The natural rainfall data were deliberately chosen to examine population dynamics under more variable and less variable conditions. The Botswana and Zimbabwe data exhibit strongly seasonal variability but also unpredictable aperiodic drought (Tyson 1986). Along with other disturbance factors, such as fire, ecologists suggest that rainfall variability and drought events in these environments imply that the attributes of more disturbed communities (Table 1) should apply. The UK, Ireland and Columbia data were chosen because these show less seasonal variation and less dramatic drought events. Ignoring other possible disturbance factors, we would expect the attributes of more stable communities to apply in these conditions. However, it should be noted that the results of these experiments cannot be seen as predictions regarding real dynamics in these regions. PLANTWORLD does not include numerous important factors such as light, nutrients and herbivory that would be required in a predictive model of this type. It is instead a model for testing the veracity of specific ecological theories. Therefore, rainfall data from real environments is used only to examine dynamics under naturally varying regimes.

4 RESULTS

4.1 EXPERIMENTS 1-6

The results of Experiments 1-6, in which all PLANTS are initiated with the *full kpon* strategy and the spatial landscape is homogeneous, are first reported. Initial populations survived under the constant regime (HH) and under UK, IRELAND and COLUMBIA rainfall. Under ZIMBABWE and BOTSWANA rainfall, the populations quickly went extinct (after 7 and 3 years, respectively). Figure 1 shows the evolution of dormancy strategies in the experiments in which initial populations survived. The bar charts show the average proportion of each dormancy strategy in the population at a particular timestep. Under the constant regime (HH) no dormancy strategy evolves throughout the run. Under UK and IRELAND data, dormancy evolves fairly rapidly and eventually *kpoff* and *ks* alleles replace all *kpon* alleles. Under both UK and COLUMBIA rainfall, *ks* alleles first evolve but then devolve being replaced by *kpoff* alleles. By the end of the run under COLUMBIA rainfall, *kpon* is still prevalent, representing an average of ≈ 7 alleles.

Figure 1 also shows the mean population sizes over 100-year intervals and the coefficient of variation[3] over 100-year, 10-year and 1-year intervals in all the experiments (1 – 6) in which initial populations survived. Given that dormancy strategies are repeated every 12 timesteps, we would expect the evolution of dormancy to most strongly effect the coefficient of variation over 1-year intervals, with less effect over 10-year and 100-year intervals. In the HH environment, no dormancy strategy evolves and population sizes remain stable throughout the run, exhibiting very small coefficients of variation over all intervals. *This behaviour corroborates classical predictions that populations will remain close to carrying capacity in constant environments.* Under UK and IRELAND data, population sizes increase as dormancy evolves, with sharp increases as the *kpoff* and *ks* alleles come to dominate. Over 100-year and 10-year intervals, coefficients of variation in these experiments increased during evolution, largely because populations are growing. As *kpoff* and *ks* come to dominate later in the runs, coefficients of variation fall over these intervals. Over 1-year intervals, coefficients of variation eventually decrease to levels similar to those exhibited under the HH environment. *These results corroborate the hypothesis that the evolution of dormancy behaviour can mitigate population level responses to environmental variability*.

Under COLUMBIA data, population initially increases. Coefficients of variation fluctuate over 100-year and 10-year intervals but do not exhibit strong decreases by the end of the run. Over 1-year intervals, the coefficient of variation has only decreased slightly from its maximum value and remains relatively high throughout the run. These results suggest that when the environment is not so variable as to select many *kpoff* or *ks* strategies (*kpon* remains prevalent in the population), populations may in fact exhibit relatively high variability (circa 25%) – considerably higher than that exhibited by populations in which dormancy comes to dominate (circa 2-3% under UK and IRELAND data). *These results suggest that if PLANTS exhibit different patterns of dormancy in different environments, knowledge of environmental variability cannot inform us of likely population dynamics.*

4.2 EXPERIMENTS 7 AND 8

As already noted, in the first experiments, when the ZIMBABWE and BOTSWANA homogeneous environments were initiated with the *full kpon* strategy, both populations quickly became extinct. In Experiments 7 and 8 we examine dynamics under the same rainfall data but in a heterogeneous environment, again initiated with the *full kpon* strategy. Since the spatial heterogeneity increases moisture variability, it is not surprising that when initiated with the *full kpon* strategy, populations rapidly reach extinction, as in the homogeneous landscape. In Experiment 9 the heterogeneous landscape under ZIMBABWE rainfall is again investigated but now we initiate all PLANTS with the *mixed strategy* (*alt. kpon/kpoff/ks*). In experiments 10 the heterogeneous landscape under BOTSWANA rainfall is again investigated, but all PLANTS are initiated with the *matched strategy*. The matched strategy represents a 'best guess' at the type of genotype likely to survive under BOTSWANA rainfall, which exhibits strongly seasonal rainfall.

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[3] The coefficient of variation = standard deviation / mean

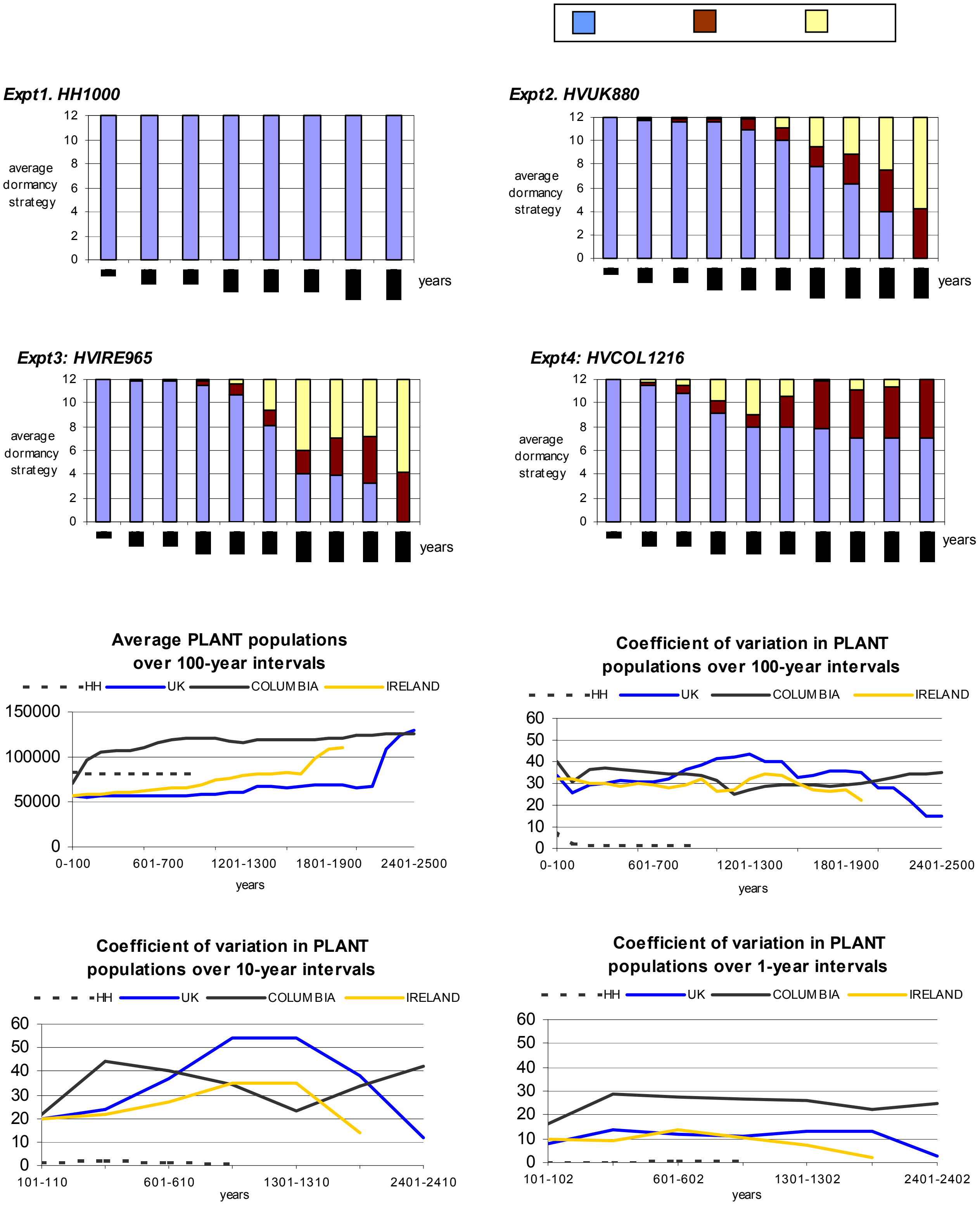


Figure 1: Results of Experiments 1 – 6: Evolution of dormancy strategies and population dynamics in various environments all initiated with 100% *full kpon* agents.

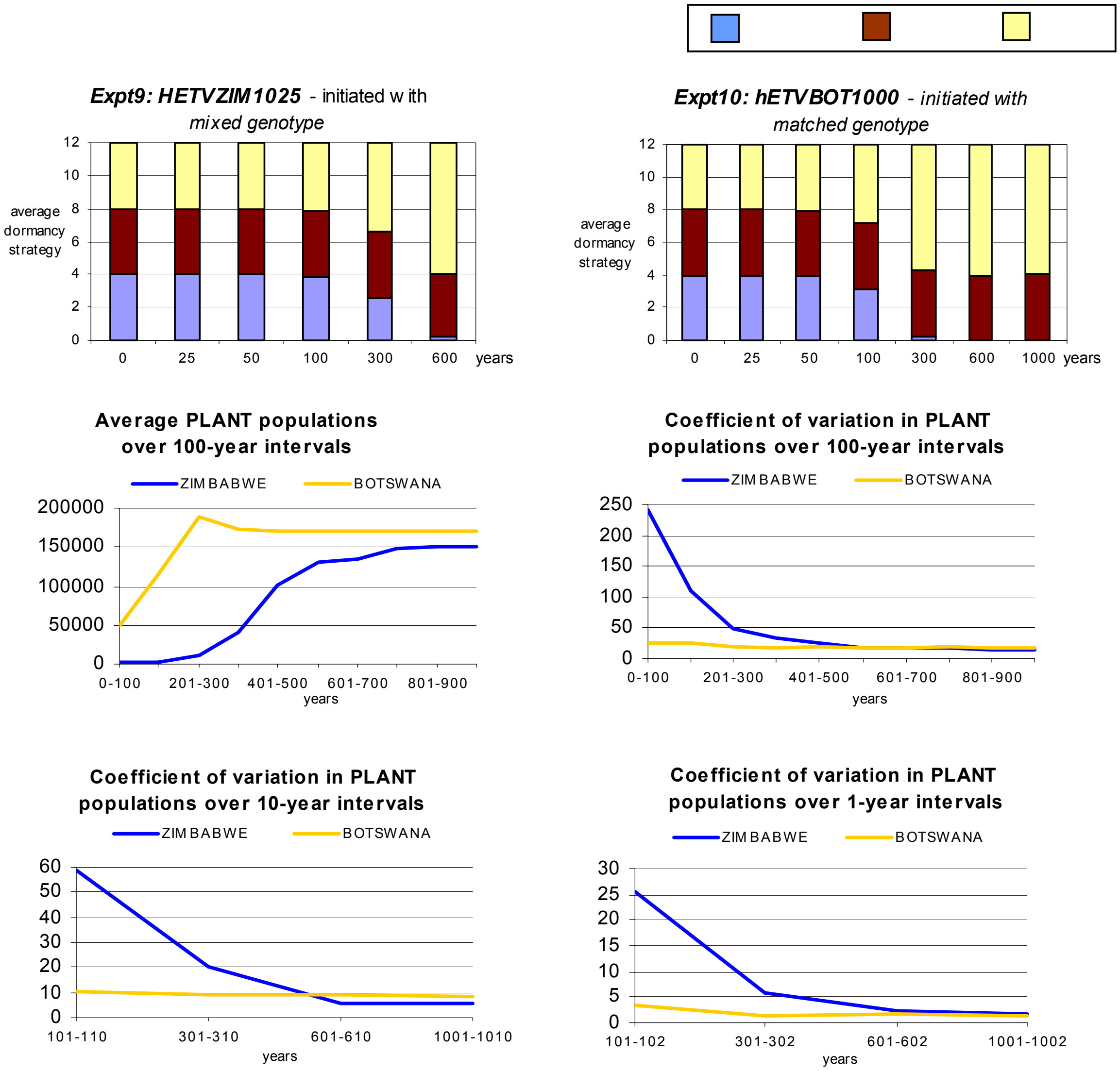
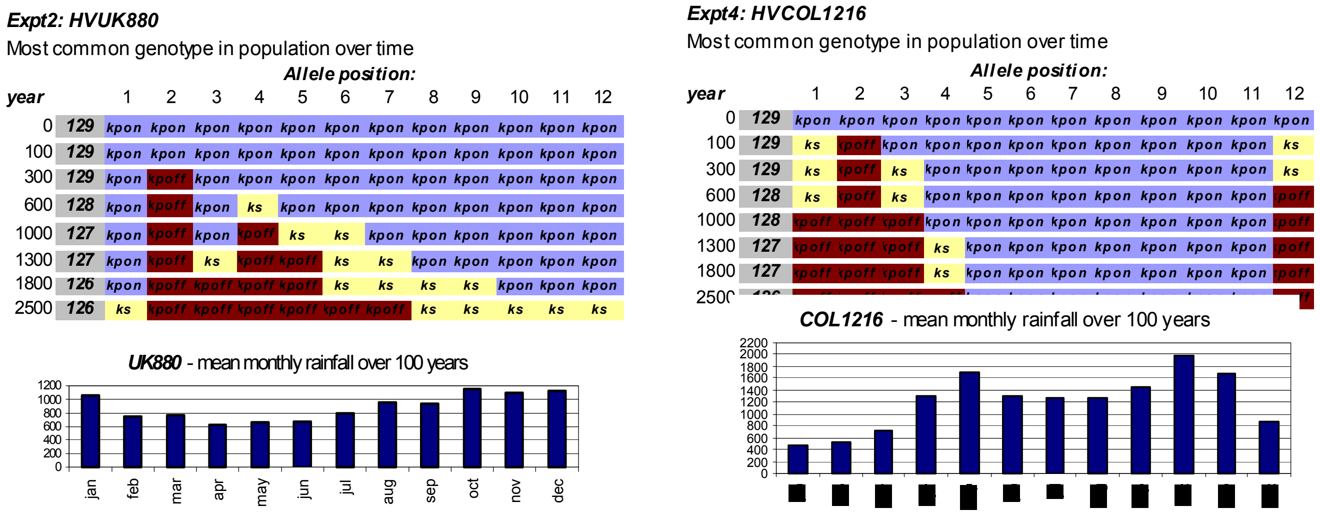


Figure 2: Evolution of dormancy and population dynamics in Experiments 7 – 10.



Expt2: HVUK880

Most common genotype in population over time

Allele position:

year		1	2	3	4	5	6	7	8	9	10	11	12
0	***129***	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon
100	***129***	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon
300	***129***	kpon	kpoff	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon
600	***128***	kpon	kpoff	kpon	ks	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon
1000	***127***	kpon	kpoff	kpon	kpoff	ks	ks	kpon	kpon	kpon	kpon	kpon	kpon
1300	***127***	kpon	kpoff	ks	kpoff	kpoff	ks	ks	kpon	kpon	kpon	kpon	kpon
1800	***126***	kpon	kpoff	kpoff	kpoff	kpoff	ks	ks	ks	ks	kpon	kpon	kpon
2500	***126***	ks	kpoff	kpoff	kpoff	kpoff	kpoff	kpoff	ks	ks	ks	ks	ks

UK880 - mean monthly rainfall over 100 years

Expt4: HVCOL1216

Most common genotype in population over time

Allele position:

year		1	2	3	4	5	6	7	8	9	10	11	12
0	***129***	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon
100	***129***	ks	kpoff	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	ks
300	***129***	ks	kpoff	ks	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	ks
600	***128***	ks	kpoff	ks	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpoff
1000	***128***	kpoff	kpoff	kpoff	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpoff
1300	***127***	kpoff	kpoff	kpoff	ks	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpoff
1800	***127***	kpoff	kpoff	kpoff	ks	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpoff
2500													ff

COL1216 - mean monthly rainfall over 100 years

Figure 3: Evolution of *ks* alleles and replacement by *kpoff* alleles under UK and COLUMBIA rainfall data.

4.3 EXPERIMENTS 9 AND 10

In both Experiments 9 and 10 populations survive and go on to evolve further dormancy (Figure 2). As dormancy evolves, populations increase and coefficients of variation fall over all intervals. Over 1-year intervals, coefficients of variation in both experiments reach levels similar to those exhibited in the HH environment and under UK and IRELAND data.

5 DISCUSSION

The above experiments corroborate the hypothesis that the evolution or pre-adaptation of functional responses to environmental variability can mitigate population variability. The only environment in which dormancy did not evolve was under the fully homogeneous and constant (HH) regime. In a further experiment (data not provided due to lack of space) we examined the effect of changing the costs, [*kpoff*] and [*ks*]. We found that even if costs are very small (0.001 and 0.002) respectively, no dormancy evolves in the HH environment. However, if costs are zero, both *kpoff* and *ks* alleles do evolve in the HH environment, slowly coming to dominate by year 1300. Since we would expect dormancy strategies to always carry some costs, we should conclude that these would not evolve in a fully homogeneous and constant environment. However, no real environment exhibits 100% constancy over all scales so that the evolution of dormancy is plausible in any real environment and will always be a tradeoff between costs and benefits.

In all experiments in which *kpoff* and *ks* evolve to dominate, coefficients of variation tend to fall, and markedly so over 1-year intervals. Even under the low and highly variable BOTSWANA data and the spatially heterogeneous landscape, the matched strategy easily survives and the population exhibits low coefficients of variation. On the other hand, when *kpon* remains prevalent, as under COLUMBIA rainfall, coefficients of variation over all intervals remains high. Presumably, the costs of evolving high dormancy outweigh the benefits in this environment, because variability is not so high as to make a high dormancy strategy worthwhile. However, since there is some level of variability in the COLUMBIA data, populations with low dormancy will exhibit numerical responses since functional responses are not prevalent.

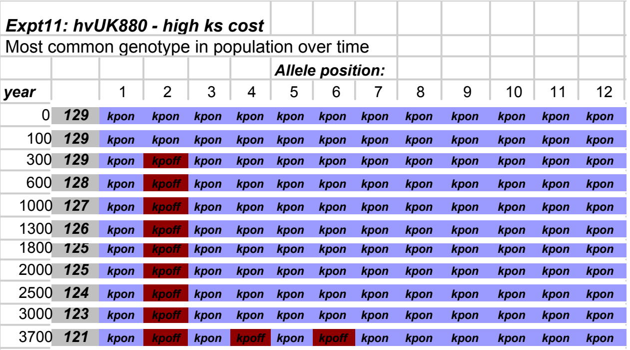
In PLANTWORLD, evolution of dormancy behaviour 'couples' organisms to their environment, and thereby 'decouples' populations from environmental variability. Whether such behaviour evolves depends on the relative costs and benefits of particular strategies in particular environments. If individual behaviour can mitigate the effects of environmental variability at the population level, then the predictions outlined in Table 1, regarding the attributes of organisms, populations and communities in contrasting environments, do not necessarily follow. We cannot therefore expect to predict organismic, population or community dynamics and organisation only on the basis of knowledge about the relative stability or instability of the environment. Indeed, it could be argued that such predictions are founded on rather anthropocentric views, under which, what constitutes disturbance for our species is assumed to constitute disturbance for other species. Taking an *organismic-eye* view of the environment implies including behaviour in ecological models, without which we fail to take account of the adaptive nature of living systems.

5.1 ADDITIONAL OBSERVATIONS

As noted in the results section, in some experiments we witness initial evolution of *ks* alleles and later replacement by *kpoff* alleles. Figure 3 shows this behaviour graphically.

Each row represents the most common genotype in PLANTWORLD at a given timestep. Under UK data, *ks* is replaced by *kpoff* in allele positions 3, 4, 5, 6 and 7. Under Columbia data, *ks* is replaced by *kpoff* in allele positions 1, 3, 4 and 12. The average monthly rainfall data below illustrates how dormancy strategies tend to evolve first to correspond with lower average rainfall months. The initial evolution of *ks* and subsequent replacement by *kpoff* is somewhat surprising, since each *ks* allele incurs twice as much cost to maintenance as each *kpoff* allele. This result suggests that population-level attributes may be feeding back to constrain agent evolution. In other words, it may be that in an environment that contains high *kpon* prevalence, PLANTS with *kpoff* alleles are less competitive since they may miss opportunities to gain resources and take longer to reach reproductive stage. However, while the cheaper *kpoff* strategy may be less competitive, the expensive *ks* strategy evolves rapidly in the above experiements. This suggests that the expensive *ks* strategy is worthwhile when competing against high prevalence of the *kpon* strategy. Even though each *ks* allele is expensive, it confers the adavantage of gaining resources when they are available, yet surviving when they are not. Thus, while PLANTS with some *ks* alleles will grow considerably slower than PLANTS with full *kpon* strategy (because of costs to maintenance and lack of growth during dormancy) their ability to survive a resource-scarce timestep means that *ks* alleles rapidly come to dominate the positions in the genome that correspond to lower average monthly rainfall. Later on in evolution, the population contains many more *ks* alleles. Under these conditions, *kpoff* appears to become more competitive at the allele positions where *ks* has previously evolved. This suggests that the ability to exhibit obligate dormancy becomes competitive only when the population is dominated by PLANTS exhibiting *ks* alleles at that locus, presumably because its low costs outweigh the benefits of the ability to be active should resources be available.

To test these ideas, we conducted further experiment under UK data in which the costs of *ks* alleles were unfeasibly high (i.e. the evolution of just one *ks* allele makes maintenance requirements > maximum utilisation) so that effectively, the *ks* strategy can not evolve. These experiments demonstrate that in the absence of *ks* evolution, the *kpoff* strategy took considerably longer to evolve (Figure 4) except in allele position 2. We can conclude, therefore, that in PLANTWORLD, population-level effects can feedback to influence subsequent evolution. As in nature, fitness is determined by biotic, as well as abiotic, aspects of the environment. The organism's biotic environment does not only include ecological interactions such as predation or interspecies competition, but also the attributes of the populations to which the organism belongs. This implies changing fitness functions during evolution even though the physical environment is not changing over evolutionary scales (Levin 1992). Such effects feedback to influence phenotypic behaviour and thereby influence population dynamics, so that cause and effect flow simultaneously back and forth between levels in the biological hierarchy. Again, this confirms the hypothesis that knowledge of abiotic features of the environment alone provides little or no predictive power regarding either population dynamics or attributes of organisms, populations or communities in different abiotic environments.



Expt11: hvUK880 - high ks cost

Most common genotype in population over time

						Allele position:							
year		1	2	3	4	5	6	7	8	9	10	11	12
0	***129***	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon
100	***129***	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon
300	***129***	kpon	kpoff	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon
600	***128***	kpon	kpoff	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon
1000	***127***	kpon	kpoff	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon
1300	***126***	kpon	kpoff	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon
1800	***125***	kpon	kpoff	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon
2000	***125***	kpon	kpoff	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon
2500	***124***	kpon	kpoff	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon
3000	***123***	kpon	kpoff	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon	kpon
3700	***121***	kpon	kpoff	kpon	kpoff	kpon	kpoff	kpon	kpon	kpon	kpon	kpon	kpon

Figure 4: Evolution of *kpoff* strategy when *ks* is an unfeasible strategy

6 CONCLUSIONS

In conclusion, these experiments in PLANTWORLD confirm the following hypotheses:

a) the evolution of dormancy behaviour can mitigate population–level responses to environmental variability

b) Population-level attributes (the frequency of particular behaviours) can feed forward to influence subsequent evolutionary dynamics.

c) It is not possible to derive organismic, population or community attributes simply from knowledge of environmental regimes.

The inclusion of evolvable behaviour in ecological models is only now becoming feasible and appears to be germane to our better understanding of both evolutionary and ecological dynamics and organisation.

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