Modelling Cultural Diversity as a Function of Environmental Stability

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Introduction

Studies have observed global and continental scale correlations between regions of high levels of cultural diversity and those with high levels of biodiversity and other related environmental factors. This correlation is believed to be vital because of its implications for the *"understanding of processes of human cultural diversification and their relationship to evolutionary and ecological mechanisms"* (Collard & Foley 2002).

Specific correlations that have been observed include a positive correlation of cultural or linguistic density (numbers of cultural groups or separate languages per unit area) with lower latitudes ($r = .93$, $p < .001$, Collard & Foley 2002); higher mean temperature ($r = .84$, $p < .001$, Collard & Foley 2002) and rainfall ($r = .86$, $p < .001$, Collard & Foley 2002; Birdsell 1953), which serve as a proxy for higher productivity, biomass, and available energy; lower climatic variability (Nettle 1998); species richness (various taxa: birds, mammals, vertebrates, flowering plants) (Sutherland 2003; Harmon 1996); habitat diversity ($r = .67$; Mace & Pagel 1995); geographic barriers such as mountains and water bodies (Nichols 1992); and proximity to aquatic resources (near coastline, river or lake) (Manne 2003; Nichols 1992). A related positive correlation holds between human population density and species richness (Gaston 2005): 1/6 of world's people live in the top 25 "hotspots" for biodiversity, constituting only 1.4% of the land area.

A variety of explanations have been proposed for the correlation with biodiversity. Several of these can be grouped under the heading of 'resource partitioning and niche formation,' wherein greater carrying capacity both allows larger human population density and necessitates greater resource partitioning, while finer niche specialization by humans is made possible by larger numbers of species or habitats (Mace & Pagel 1995; Novotny & Drozd 2000; Moore *et al.* 2002; Collard & Foley 2002; Turner *et al*. 2003).

Hunn suggests that tropical regions foster greater human population density, which leads to more splitting of populations into new groups because humans have an innate affinity for groups of a certain size (about 500 people[1]), and thus tend to split at this level if resources allow (Hunn 1994). Harmon proposes that the coevolution of interacting species, habitats, and human cultural approaches leads to the observed correlations (Harmon 1996). Nettle suggested that lower climatic variability (greater stability) allows smaller groups to survive; more variability translates into greater risk of starvation, which groups of people mitigate by expanding their range and maintaining broad networks of relationships with others (Nettle 1998, 1999).

Nichols (1992), Mace & Pagel (1995), and Collard & Foley (2002) hypothesize that there is a natural trajectory over time after settlement of a region by humans: a long gradual diversification as groups split and new cultures develop. Nettle (1998) refines this idea by adding that initial diversification is followed by long, gradual consolidation with loss of cultures. A more specific reason for loss of cultures is given by Moore *et al*. (2002) and Collard & Foley (2002): they observe that dominant monolithic cultures have eradicated much cultural diversity in certain parts of the world (China, Europe, US, parts of Africa), and that agricultural expansion wiped out both cultures and species.

Few of these proposed explanations have described or documented a precise mechanism by which biological diversity can lead to cultural diversity. The goal of our study was to see if any of the proposed mechanisms was plausible; i.e. if a simplified quantitative model of the mechanism could be shown to result in the observed correlation. If so, the essential components of the mechanism (elements of the model) could be predicted to exist, and tested with real-world observations.

The mechanism we chose to model was the effect of environmental stability or variance on cultural diversity, mentioned above. Although it is not a part of our model, there is an underlying assumption of correlation (and perhaps causality) between environmental stability and biological diversity (Gaston 2005; Moore *et al.* 2002). If environmental stability can be shown to foster cultural diversity, this could account for the correlation between cultural and biological diversity, at least in part.

Methods

In order to model this mechanism, we made a number of simplifying assumptions. Our human populations were conceived of as nomadic hunter-gatherer bands engaged in immediate-return foraging--prior to agriculture, money economies, and the demographic transition. While many studies of cultural diversity count numbers of defined languages or distinct cultures, we simply used number of population groups as a proxy for cultural diversity. We coded the model as an agent based simulation, developed in Matlab, in which individual population groups are considered the agents. No spatial dimension or grid was incorporated.

The logic of our model was as follows: groups of people live on the landscape, subsisting on resources generated by environmental productivity. When resources are plentiful, populations grow and groups eventually split at some upper threshold population size. When resources are limiting, populations shrink and groups eventually go extinct (or merge with others) after falling under some lower threshold population size. Thus the pattern of productivity from year to year (stable versus fluctuating) should influence the size attained by groups and the number of groups that survive.

The model was initialized with a specified number of groups (100), each with a specified population assigned by a random normal generator (with mean 50 and variance 20). The level of environmental stability was assigned in the model as either stable (no variance) or unstable (low, medium or high variance) for each simulation trial run. The level of environmental stability in turn determines the annual productivity each year via a random generator which is given probabilities of very good, good, normal, bad, or very bad years. Expected value of total productivity per unit area is equal for all environment types. For the high variance environment, productivity varies from year to year with a standard deviation of 47% of mean. The given probabilities and levels of productivity used were as follows:

Environment	Type of year	Probability	Productivity*
Stable	Very Good	0	175 units
	Good	0	135 units
	Normal	1.00	100 units
	Bad	0	65 units
	Very Bad	0	25 units
Low Variance	Very Good	.05	175 units
	Good	.15	135 units
	Normal	.60	100 units
	Bad	.15	65 units
	Very Bad	.05	25 units
Medium Variance	Very Good	.10	175 units
	Good	.20	135 units
	Normal	.40	100 units
	Bad	.20	65 units
	Very Bad	.10	25 units
High Variance	Very Good	.15	175 units
	Good	.20	135 units
	Normal	.30	100 units
	Bad	.20	65 units
	Very bad	.15	25 units

* Note that productivity was expressed as units biomass produced annually per unit area. The area was standardized at 200 km^2 across all trials.

Per capita resource allocation is equal within and between groups. However, larger groups are penalised each year by way of reduced availability of resources per person. Hence as group size increases, groups lose a higher fraction of their overall resources. This penalty is an abstraction of the social cost involved in sustaining larger groups. The penalty incurred by populations for larger group size is given by:

$$y = 0.00001x^2 + 0.0485x - 2.3873$$

where x is the population size for a given year and y is the percentage penalty on available productivity applied to each group. This penalty is negligible at a population of 50, and amounts to approximately 25% of resource allocation when groups reach a population of 500—the observed upper end for hunter-gatherer populations.

After allocating resources and imposing the group size penalty, populations grow or decline according to the following functions:

When resources per capita ≥ 1.0, percentage growth of populations is given by:

$$\boldsymbol{a = 3.6108 * \log_e (b) + 1.1319}$$

where ***b*** is the resources available per person and ***a*** is the percentage growth of the population group. When resources are abundant and carrying capacity has not been reached, this function results in an upper annual growth rate asymptote at about 3%, which is in accord with literature estimates of unconstrained human population growth.

When resources per capita < 1.0, percentage decline of populations is given by:

$$\boldsymbol{a = 62.794 * \log_e (b) + 7.0504}$$

where ***b*** is the resources available per person and ***a*** is the percentage decline of the population group. This function results in an ever-increasing rate of decline as resources fall farther below the needed 1.0 per person.

As populations decline, they can reach a lower threshold, defined as the population size below which there is a specified probability of groups going extinct. The remaining groups below this threshold merge with randomly selected other groups. This lower population threshold, set at 25 in our trial runs, reflects the minimum necessary population for a typical hunter-gatherer society to carry out the necessary functions of hunting, foraging, reproduction and childcare.

A central feature of our model is that each group has a specific upper threshold preference, defined as the group population size at which the group will split to maintain a viable social structure. This upper threshold represents the observed tendency of hunter-gatherer groups to fission when they feel they have gotten too large, often due to internal argument and conflict. For simplicity, groups split into two groups of equal size. Subsequent to splitting, the upper threshold preference of the parent group is passed on to the two daughter groups as a cultural trait. When groups below the lower threshold merge, the resulting group carries an upper threshold preference which is a weighted mean of the preferences of the two merging groups. A range of initial upper threshold preferences for the original 100 groups in the simulation is specified at the beginning of each trial run.

After some experimenting with various parameter values to learn how the simulation behaved, we settled on four main trials to determine whether there were any sets of conditions in which the model resulted in greater cultural diversity under conditions of greater environmental stability. We had learned through experimenting with the model that low, medium and high variance environments behaved in essentially the same way (which was very different from that of the stable environment). Thus for each of the trials we just ran the simulation with a stable environment (only 2000 time steps or years were needed to see trends), and high variance environment (20000 years needed to see trends).

Results

Results for the four trials we conducted were as follows. Note that in each case, results are provided for (a) the stable environment, and (b) the high variance environment. These figures may be seen in the attached pdf document.

Trial 1. BASELINE

Rationale: This is what we consider to be the most realistic set of parameters for the simplified model. Most groups have the opportunity to merge with other groups if they fall below the threshold. Large groups are penalized some fraction of resources to maintain their social structure and relationships. Different groups have different cultural preferences for maximum size of group ("upper threshold preference").

Parameters:

25% probability of extinction if under threshold
Group size penalty of 1% @ 75, 25% @ 500
Upper Threshold Preferences initially set at 100,150,200,250,300 (evenly distributed)

Total Population:

For stable environment, total population (Figure 1a) goes quickly up to 22000 (within 100 years) and is very stable after that.

For high variance environment, total population (Figure 1b) shows continual fluctuation between 5800 and 12,000 (sometimes up to 16000 or 20000).

Mean Group Population:

For stable environment, mean group population (Figure 2a) rises from 65 to 120, then quickly falls to 97 and is completely stable in 100 years.

For high variance environment, mean group population (Figure 2b) fluctuates within certain ranges (30 – 95) which change from time to time—apparently in response to big extinction events which alter the distribution of group population sizes; doesn't seem to reach a set range in the 20000 time span of simulation.

Group Number

For stable environment, group number (Figure 6a) rises from 100 to 222 in under 100 years, then stabilizes.

For high variance environment, group number (Figure 6b) fluctuates on either side of 120 for a while, then rises to around 170 for a while, then falls to 120 for a while (to end of simulation); seems to undergo these phase shifts in response to the same extinction events that alter mean group size.

Mean Upper Threshold Preference
For stable environment, mean upper threshold preference (Figure 7a) falls rapidly (within 100 years) from an initial mean of around 200 to a stable value of about 160. Weighted mean confirms this.

For high variance environment, mean upper threshold preference (Figure 7b) bounces around between 170 to 190 for first 8000 years (gradually declining), then gets more stable for the rest of the time at around 172. Weighted mean confirms this.

General
During the transient, the total population stabilizes before the number of groups stabilizes; consequently, group size overshoots the equilibrium at first, and is then brought back down to the stable size (~97) through splitting (as groups exceed their UTP).

Group population size seems to run along in one state for some time, then gets kicked into another state (higher or lower) by big extinction events that kill off the lower population groups.

Number of groups and UTP don't ever really stabilize, but seem to get less likely to change over time.

Trial 2. 100 % EXTINCTION

Rationale: We wanted to see what the system would do when put under the pressure of certain extinction upon falling under the population threshold. This would force populations to come to terms with avoiding extinction.

Parameters:
100% probability of extinction if under threshold
Group size penalty of 1% @ 75, 25% @ 500
Upper Threshold Preferences initially at 100,150,200,250,300 (evenly distributed)

Total Population
For stable environment, total population (Figure 9a) goes quickly up to 22000 (within 100 years) and is very stable after that.

For high variance environment, total population (Figure 9b) shows continual fluctuation between 5800 and 12,000 (sometimes up to 16000 or 18000).

Mean Group Population:
For stable environment, mean group population (Figure 10a) rises from 65 to 120, then quickly falls to 97 and is completely stable in 100 years.

For high variance environment, mean group population (Figure 10b) fluctuates between 40 to 100 (and sometimes up over 120) throughout the time frame of the simulation.

Group Number
For stable environment, group number (Figure 13a) rises from 100 to 225 in under 100 years, then stabilizes.

For high variance environment, group number (Figure 13b), after some initial fluctuation, seems to stabilize at about 132 for the rest of the simulation.

Mean Upper Threshold Preference
For stable environment, mean upper threshold preference (Figure 14a) falls rapidly (within 100 years) from an initial mean of around 200 to a stable value of about 160. Weighted mean confirms this.

For high variance environment, mean upper threshold preference (Figure 14b), after some initial fluctuation for the first 3500 years, stabilizes at around 192. Weighted mean confirms this.

General
For variable environment, every time we ran it, we got something different (stochastic environment probably drives this). If by chance there are too many very bad years in a short time span, all the populations can actually be driven to extinction.

In a stable environment, group number (225) and group size (97) rapidly reach an equilibrium or steady state, and do not change after that. It is basically identical to results for 25% extinctions, since extinction almost never happens anyway.

Trial 3. REDUCED UPPER THRESHOLD PREFERENCE

Rationale: We decided to run with 20% of groups at a lower Upper Threshold Preferences value than the populations seem to converge to, to see if it would destabilize the system or force a lower population equilibrium, or if these particular groups would go extinct.

Parameters:
100% probability of extinction if under threshold
Group size penalty of 1% @ 75, 25% @ 500
new set of initial Upper Threshold Preferences (60, 150, 200, 250,300) – note that 60 is below the group size that populations tended to stabilize at in the previous trial (with lowest Upper Threshold Preference at 100).

Total Population
For stable environment, total population (Figure 16a) goes quickly up to 22000 (within 100 years) and very stable after that.

For high variance environment, total population (Figure 16b) shows continual fluctuation between 5800 and 12,000 (sometimes up to or above 16000).

Mean Group Population:
For stable environment, mean group population (Figure 17a) rises from 50 to 95, then quickly falls to 55 again and stabilizes (in first 100 years).

For high variance environment, mean group population (Figure 17b) fluctuates between 50 and 100 the first 4000 years, then between 60 to 120 (sometimes going over 160) for the rest of the simulation.

Group Number
For stable environment, group number (Figure 20a) quickly rises to about 400 and stabilizes.

For high variance environment, group number (Figure 20b) after a bit of fluctuation, runs at about 117 for a few thousand years, then adjusts downward to about 88 groups (after a big extinction event that apparently kills off all the smaller groups).

Mean Upper Threshold Preference
For stable environment, mean upper threshold preference (Figure 21a) drops from 200 to around 105 in the first 100 years, then stabilizes. Weighted mean confirms this.

For high variance environment, mean upper threshold preference (Figure 21b), after a bit of fluctuation, runs at about 198 for a few thousand years, then adjusts upward to about 239 (after the big extinction event that kills off all the smaller groups). Weighted mean confirms this.

General
For stable environment, lowering the lowest UTP resulted in a lowering of the mean population per group (from 97 down to 55) and of the mean UTP (from 190 down to 105) and weighted mean UTP. It also resulted in a raised number of groups at equilibrium (over 400), but the exact same total population in the system.

With high variance environment, although the lowest UTP was set at 60 instead of 100, the mean UTP actually increases significantly (to 240, whereas it was ~ 190 with higher initial UTP). The mean group size fluctuates between 60-180, whereas in previous trial (UTP = 100) it ran between 40-120.

Trial 4. INCREASED UPPER THRESHOLD PREFERENCE

Rationale: We decided to try raising all group Upper Threshold Preferences to eliminate any constraint on group size, to see what the dynamics would be simply based on the interplay between group extinctions and upper group size penalty. In other words, we were trying to determine to what extent the dynamics are controlled by Upper Threshold Preferences and to what extent by extinctions of groups that grow too large and then fall too hard.

Parameters:
100% probability of extinction if under threshold
Group size penalty of 1% @ 75, 25% @ 500
all Upper Threshold Preferences at 500

Total Population
For stable environment, total population (Figure 23a) goes quickly up to 22000 (within 100 years) and remains very stable after that.

For high variance environment, total population (Figure 23b) exhibits continual fluctuation between 5800 and 12,000 (sometimes up to or above 16000).

Mean Group Population:
For stable environment, mean group population (Figure 24a) rises from around 50 to 228 (in 100 years), then stabilizes.

For high variance environment, mean group population (Figure 24b) fluctuates between 60 to 120 throughout (sometimes rising above 160).

Group Number
For stable environment, group number (Figure 27a) drops from 100 down to 89 the first year, then stabilizes.

For high variance environment, group number (Figure 27b) drops from 100 down to 96 the first year, then stabilizes.

Mean Upper Threshold Preference
As the mean UTP is always at 500, which is too high to be reached, the mean UTPs are always stable in both conditions. Therefore we do not present any plots here.

General
For stable environment, mean group size jumps way up (doubles) to 220 and is stable; thus total number of groups is greatly reduced, but still stable (89). Total population is stable at about 20,000.

For variable environment, mean group size fluctuates between 60-160, while total number of groups is completely stable (96), which is just above the number for the stable environment (89).

Table 1. Summary of Observed Results

	Trial 1 Baseline	*Trial 2 100% extinction*	*Trial 3 Reduced UTP*	*Trial 4 Increased UTP*
Total population				
Stable environment	22000	22000	22000	22000
High variance environment	~5800 – 12000 mean=7451	~5800 – 12000 mean=7533	~5800 – 12000 mean=7448	~5800 – 12000 mean=7468
Mean group population				
Stable environment	97	97	55	228
High variance environment	~30 – 95 mean=57	~40 – 100 mean=57	~60 – 120 mean=78	~60 – 120 mean=78
Number of groups				
Stable environment	222	225	400	89
High variance environment	120	132	88	96
Mean UTP				
Stable environment	160	160	105	500
High variance environment	172	192	239	500

- Total population size is controlled by environment: it is larger and stable in stable environments; smaller and fluctuates to track productivity in high variance environments.

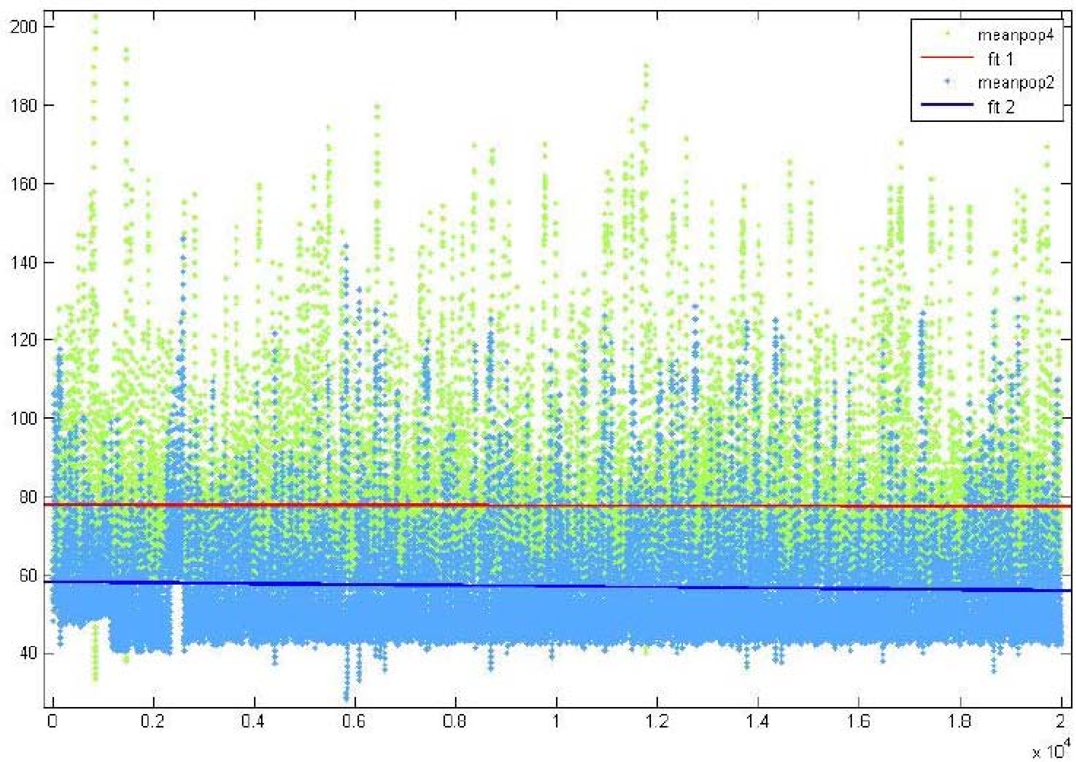
- Group population size stabilizes in stable environments, but fluctuates greatly in high variance environments from values lower to higher than that of in stable environment.

- Group size preferences tend to be lower for stable environments and are pushed higher in high variance environments.

- When the lowest group size preference is reduced, mean group sizes are pushed down.

- Number of groups in the stable environment is much larger than that in high variance environment.

Figure 28. Summary Plot of Mean Group Population in High variance Environment For Trial 2 (100% Extinction) and Trial 4 (Raised UTP)



Discussion

Many studies have shown a strong association between higher levels of human cultural diversity and higher biological diversity and related environmental factors. While several mechanisms have been proposed to explain this observed correlation, for the most part they have not been developed rigorously. Our simulation does this, and results indicate that at least one plausible mechanism exists that is capable of linking cultural diversity to one correlate of biological diversity: environmental stability. This finding should not be viewed as proof of such a causal relationship. Rather, the model should be viewed as a more clearly articulated hypothesis.

Essential components of the model include (1) a function linking population growth to environmental productivity; (2) a lower group size threshold below which groups go extinct; and (3) a range of cultural preferences for splitting (dividing) the group at some upper group size threshold. These are the key elements of the hypothesized mechanism that are required in order for it to generate the outcomes observed in the real world. As such, they constitute predictions associated with the hypothesis. To the extent that these three elements can be shown to exist in preindustrial human populations, the hypothesized mechanism gains support. Of course, other mechanisms (such as cultural niche construction) may also be at work, in addition to or instead of the effect of environmental stability.

Future work needed to more fully understand the relationship between cultural diversity and environmental stability includes both the theoretical and the empirical. Parameter space for the model needs to be explored, running the simulation with a wide range of parameter values and initial conditions to see how it behaves under these conditions. The structure of the model could be altered to incorporate spatial dimensions as well as conflict and migration between groups. Empirical data need to be collected to refine our understanding of where and when this proposed relationship holds, and to obtain real-world data against which to test the predicted "essential elements" of the model.

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Endnote
[1] Hunn's data on populations came from Birdsell, who reviewed data on hunter-gatherer populations available in the 1950's, and concluded that tribes averaged around 500 individuals, while the local band (people living and hunting together on a daily basis) typically ranged from 20 to 50, but sometimes as high as 100 individuals (Birdsell 1953, 1958).

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Figure 1a. Total Population, Stable Environment, Trial 1 (Baseline)

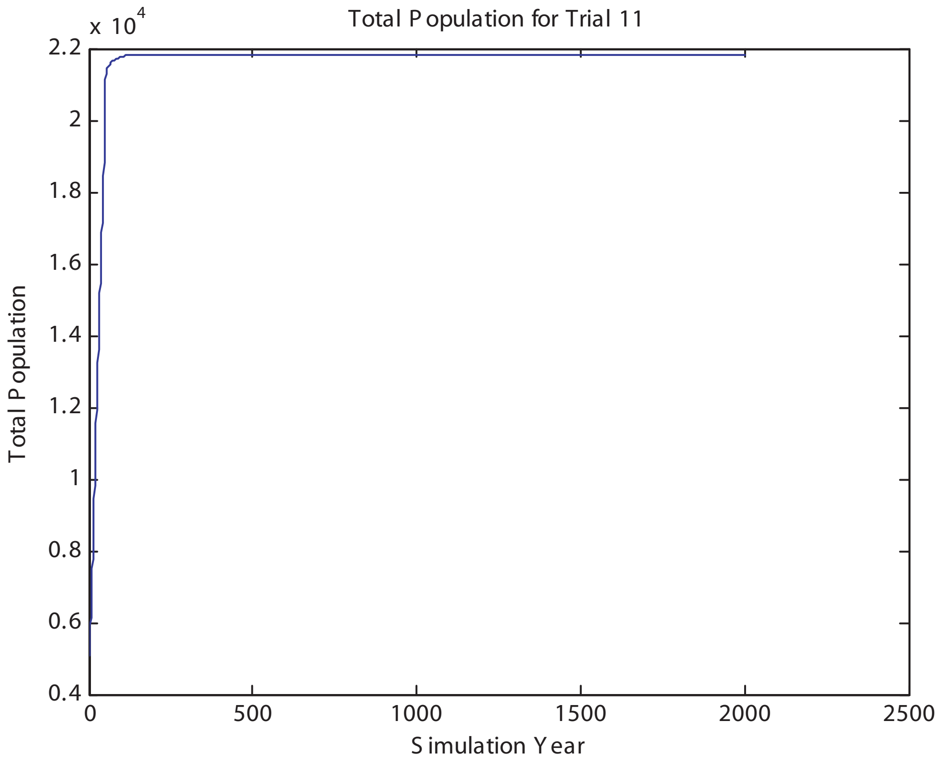

Figure 1b. Total Population, Unstable Environment, Trial 1 (Baseline)

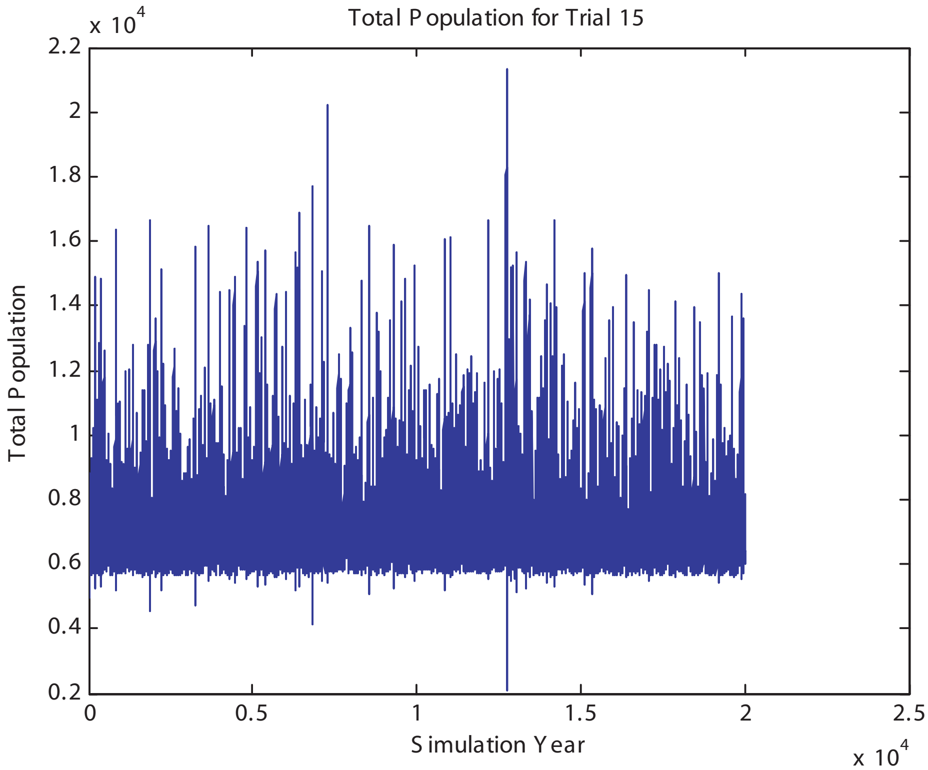

Figure 2a. Mean Group Population, Stable Environment, Trial 1 (Baseline)

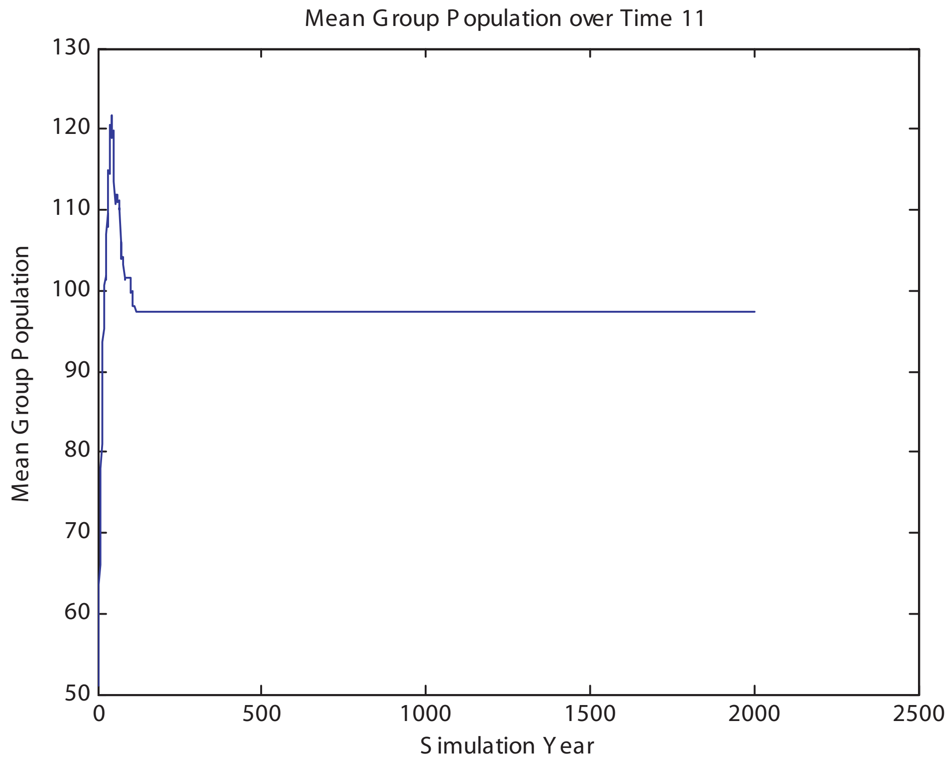

Figure 2b. Mean Group Population, Unstable Environment, Trial 1 (Baseline)

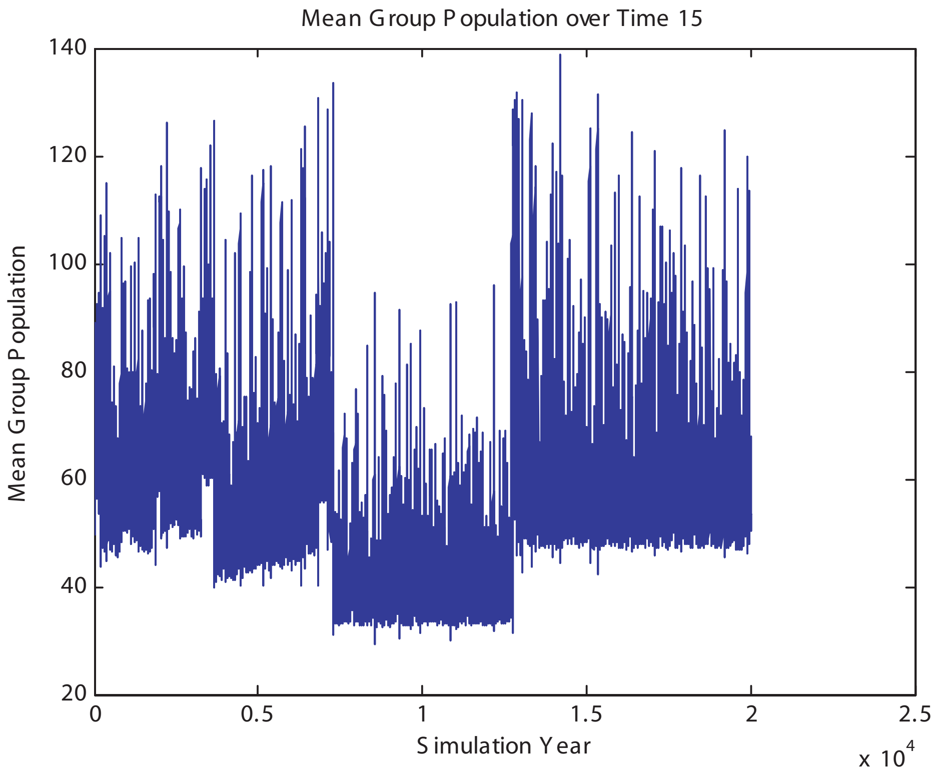

Figure 3a. Number of Extinctions, Stable Environment, Trial 1 (Baseline)

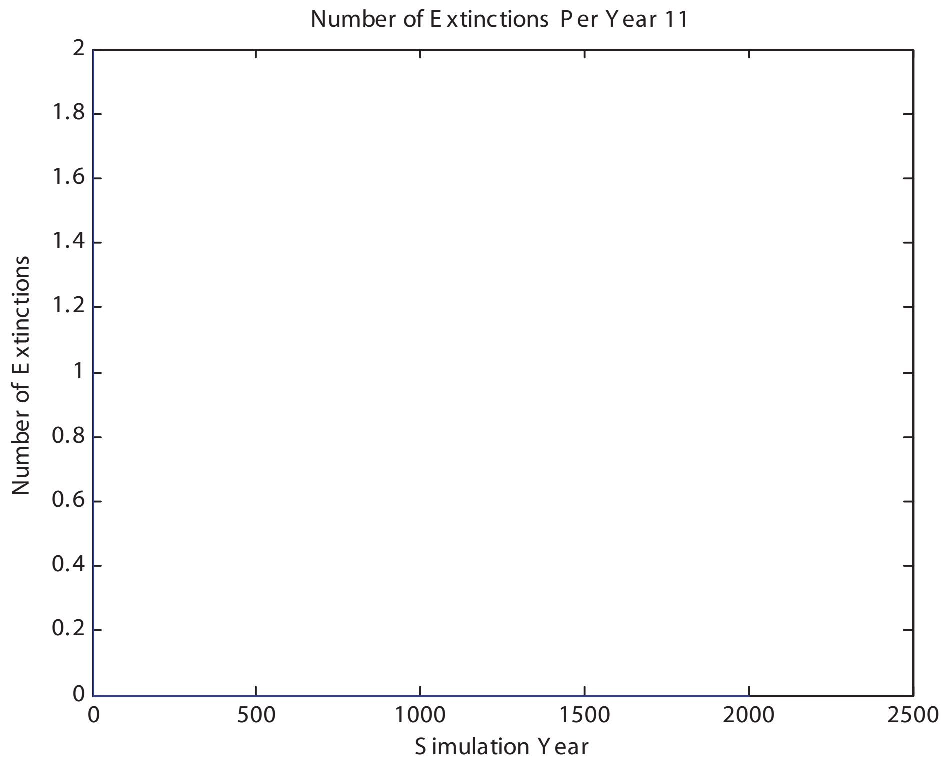

Figure 3b. Number of Extinctions, Unstable Environment, Trial 1 (Baseline)

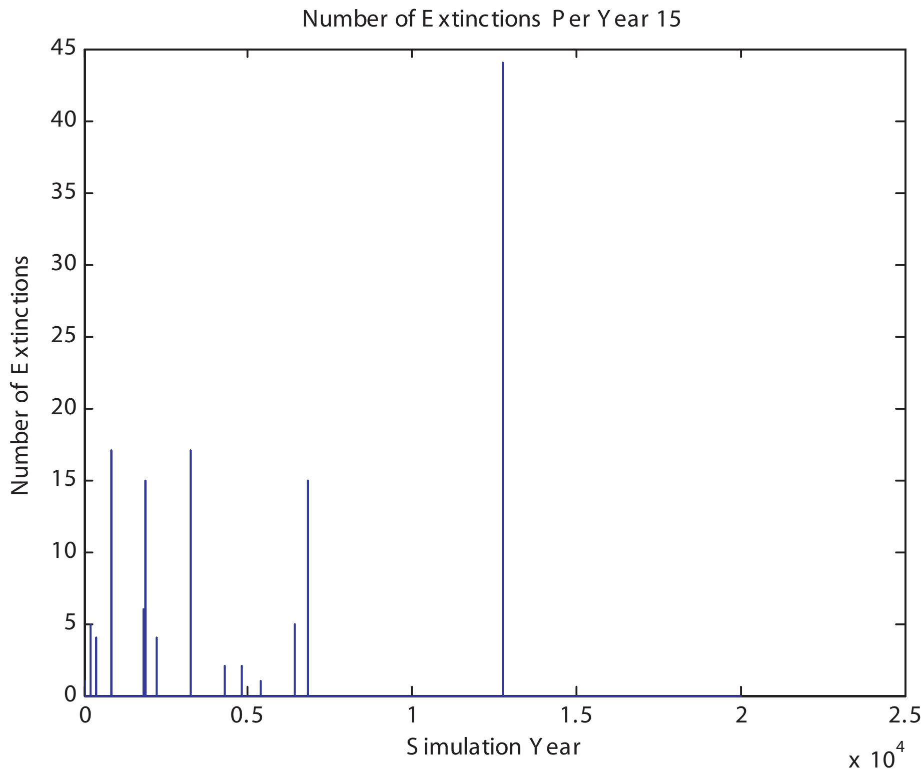

Figure 4a. Number of Mergings, Stable Environment, Trial 1 (Baseline)

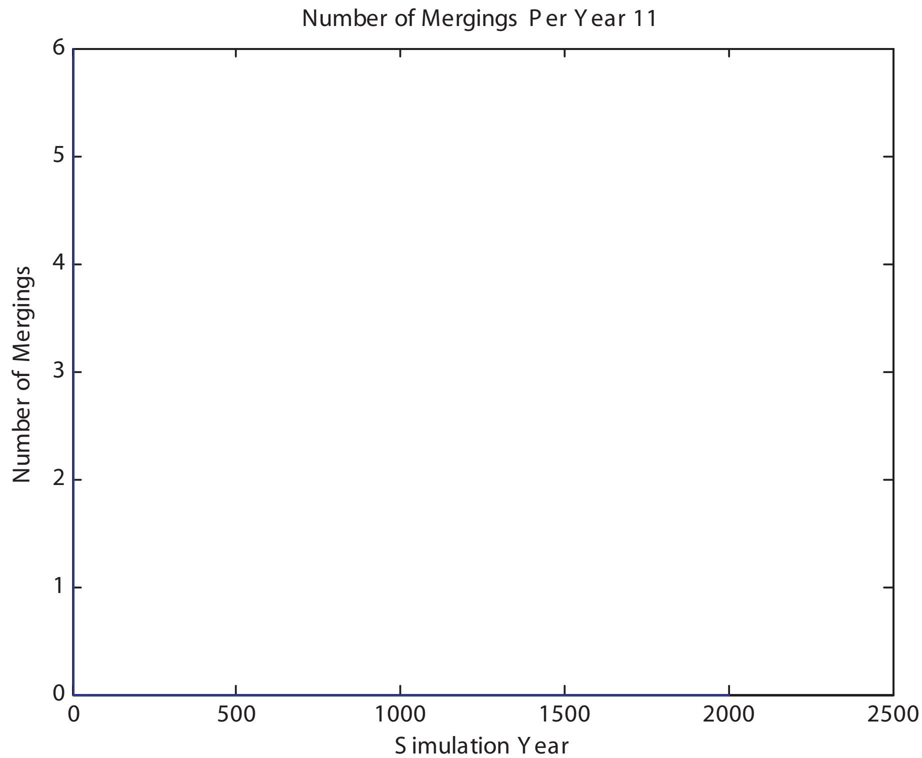

Figure 4b. Number of Mergings, Unstable Environment, Trial 1 (Baseline)

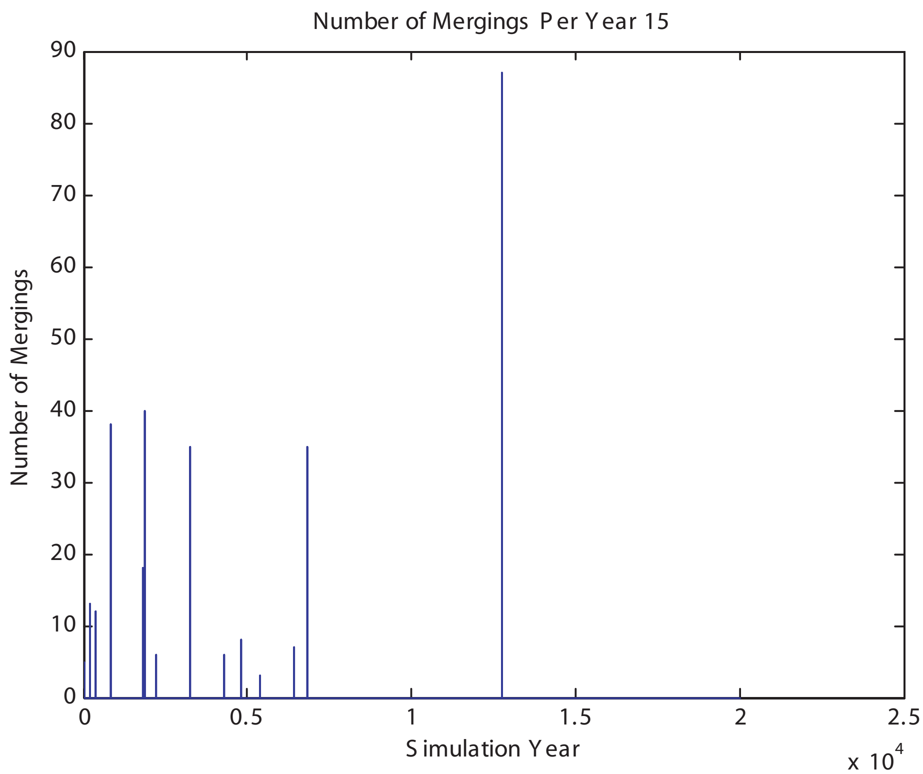

Figure 5a. Number of Splittings, Stable Environment, Trial 1 (Baseline)

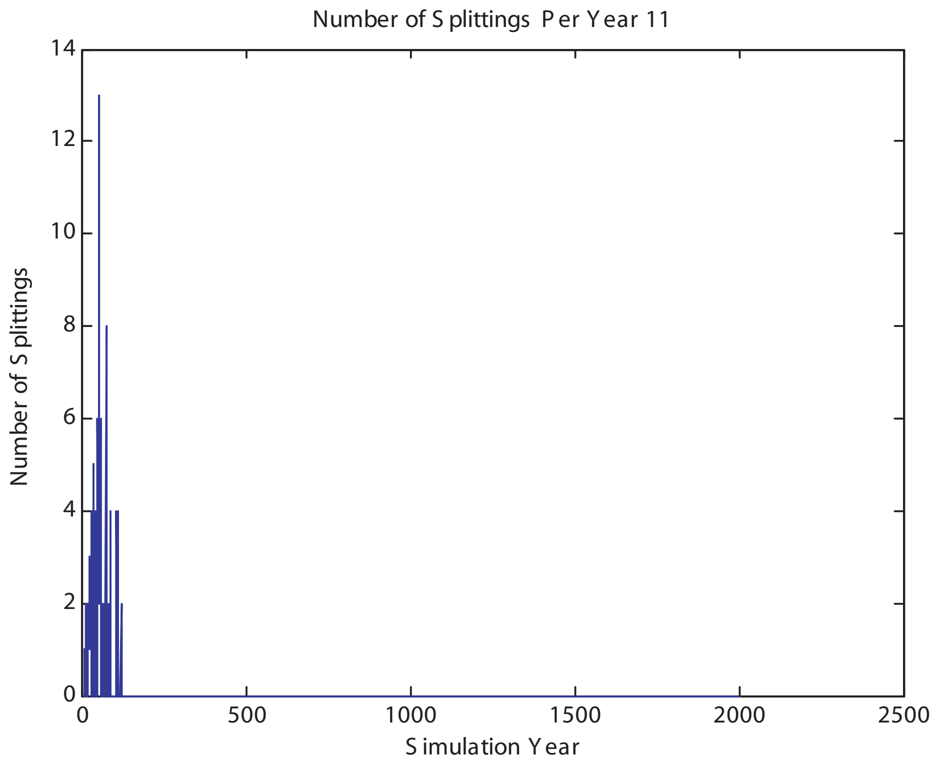

Figure 5b. Number of Splittings, Unstable Environment, Trial 1 (Baseline)

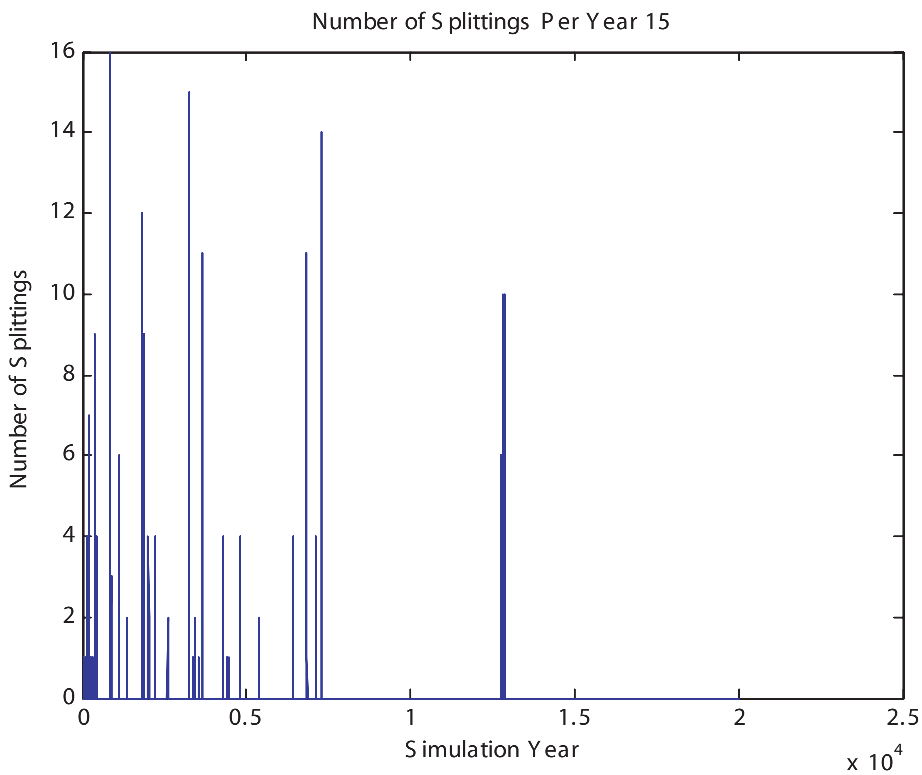

Figure 6a. Number of Groups, Stable Environment, Trial 1 (Baseline)

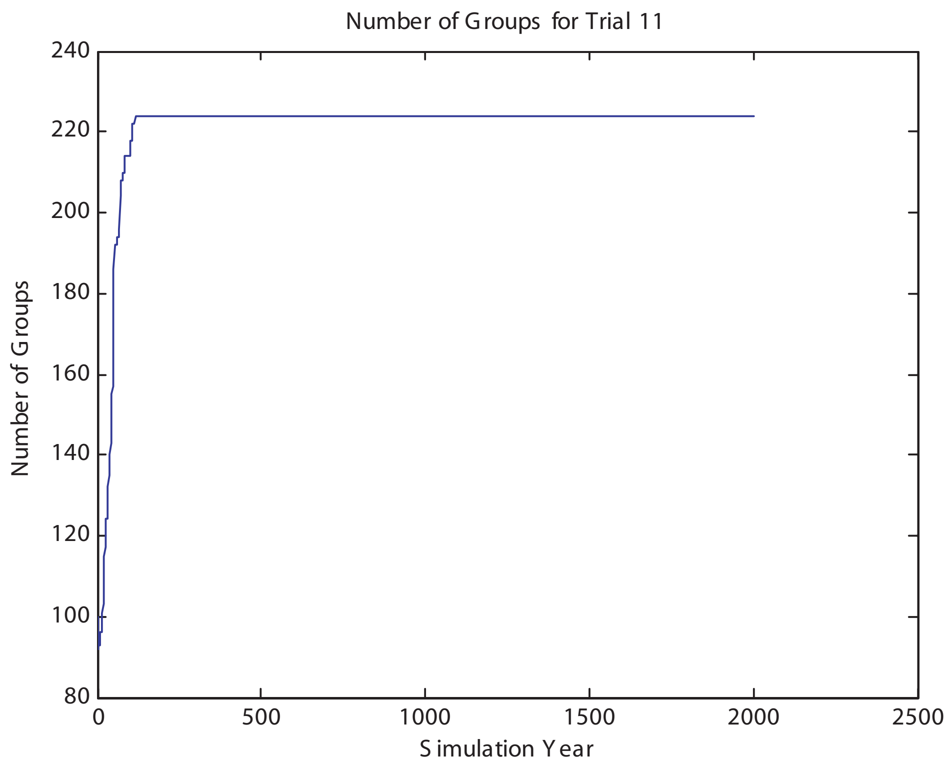

Figure 6b. Number of Groups, Unstable Environment, Trial 1 (Baseline)

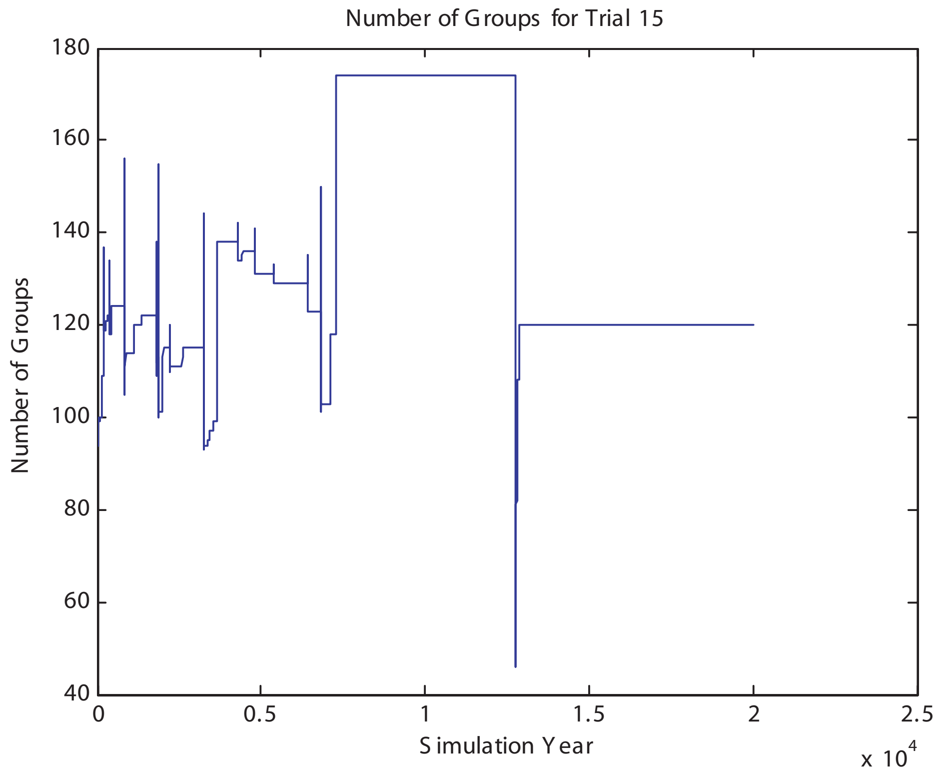

Figure 7a. Mean Upper Threshold Preference, Stable Environment, Trial 1 (Baseline)

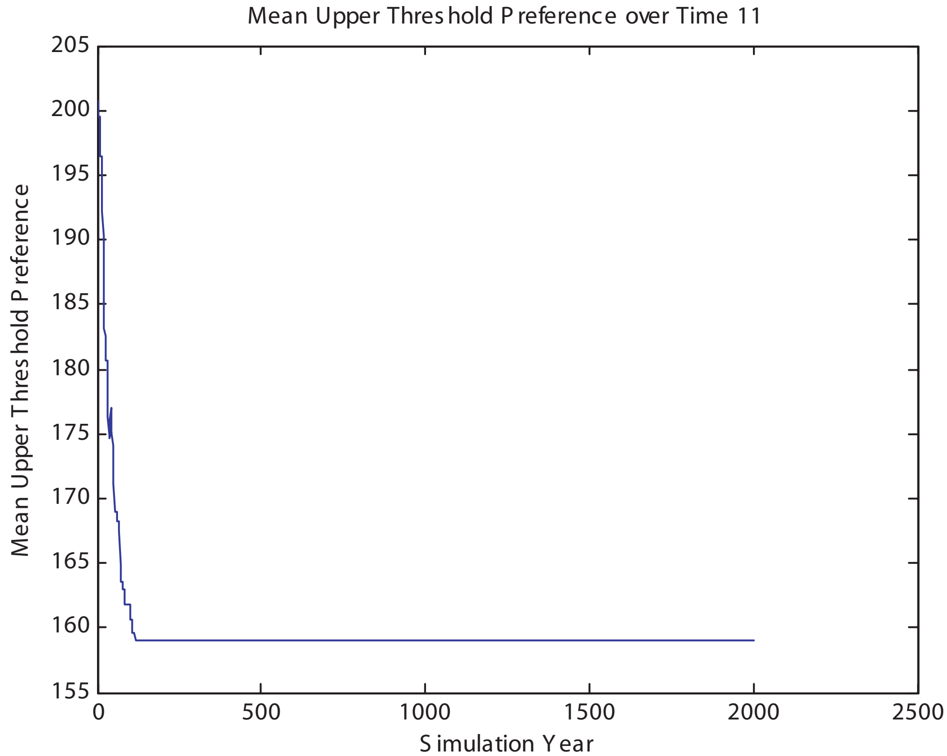

Figure 7b. Mean Upper Threshold Preference, Unstable Environment, Trial 1 (Baseline)

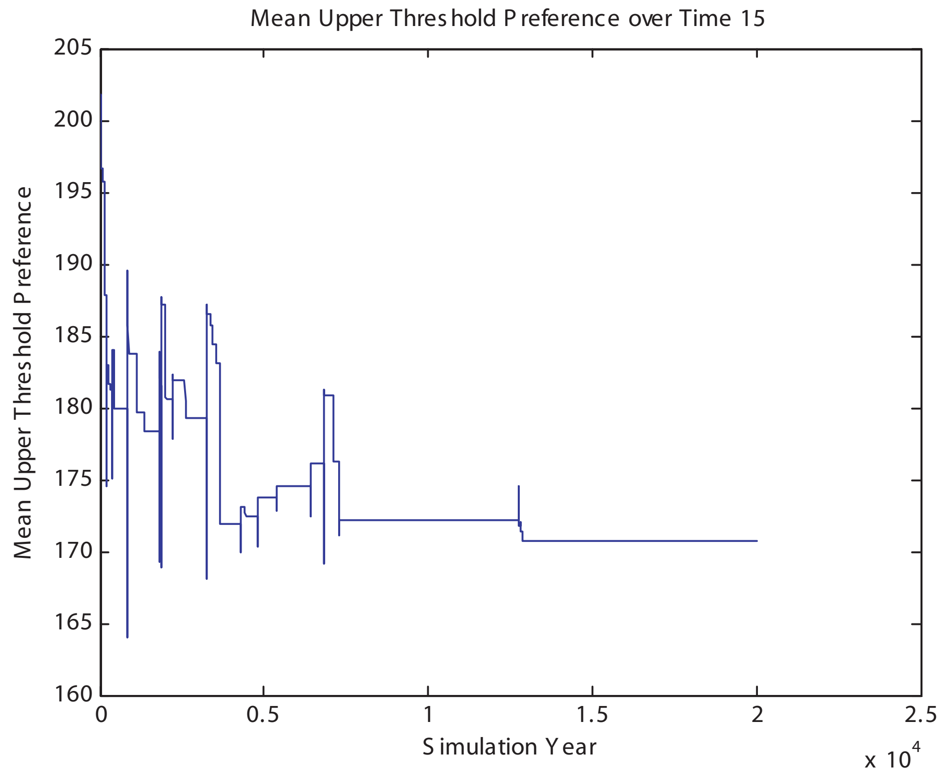

Figure 8a. Weighted Mean Upper Threshold Preference, Stable Environment, Trial 1 (Baseline)

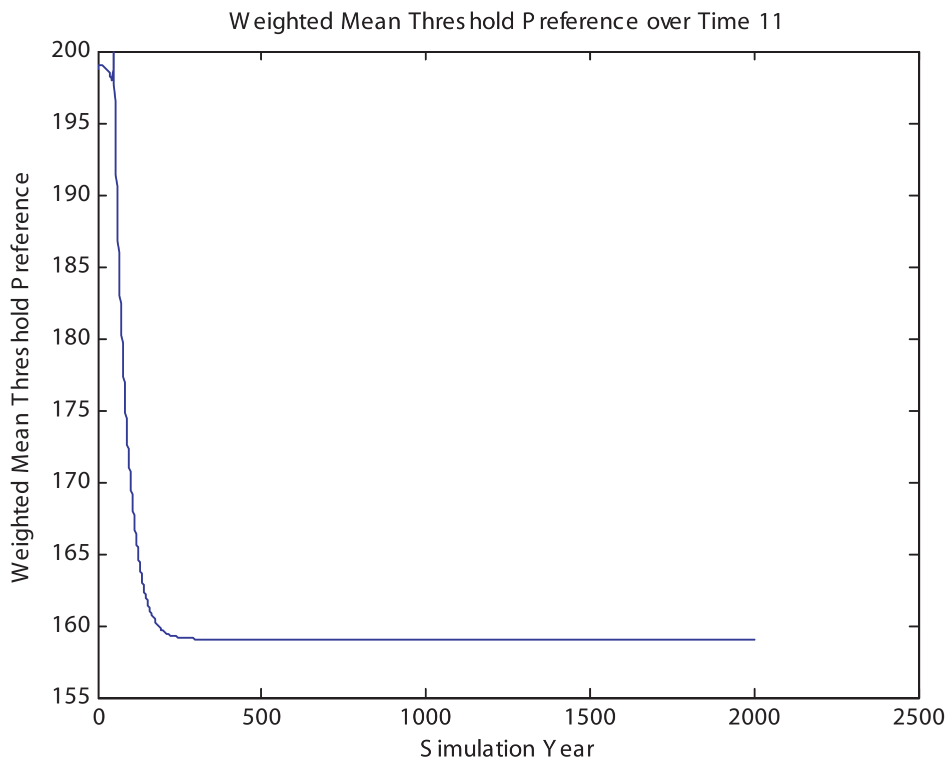

Figure 8b. Weighted Mean Upper Threshold Preference, Unstable Environment, Trial 1 (Baseline)

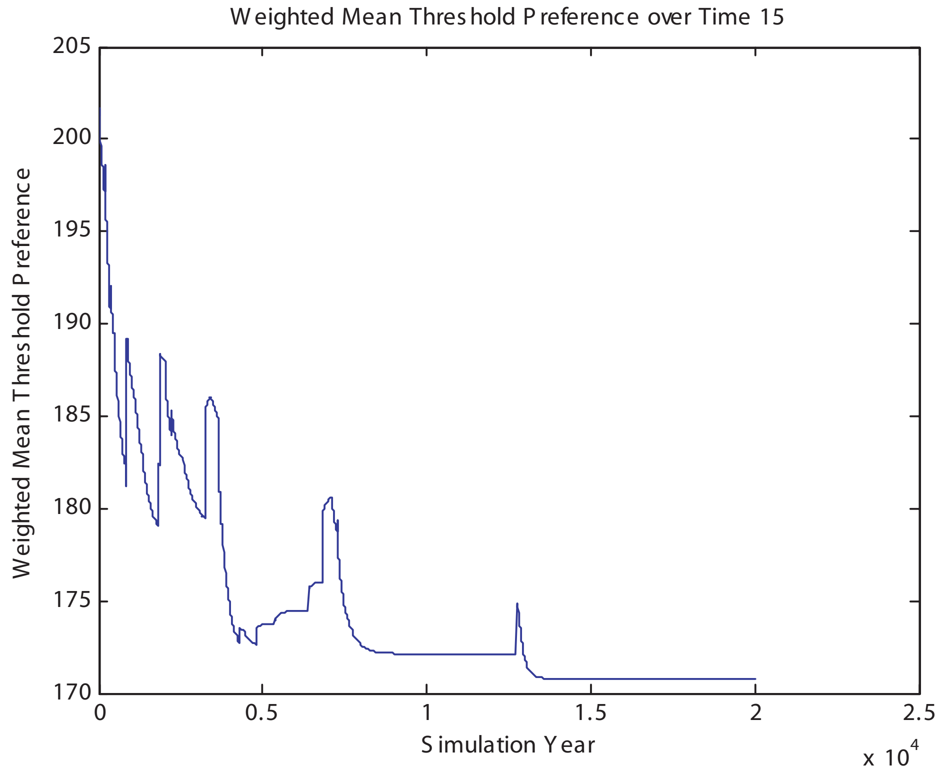

Figure 9a. Total Population, Stable Environment, Trial 2

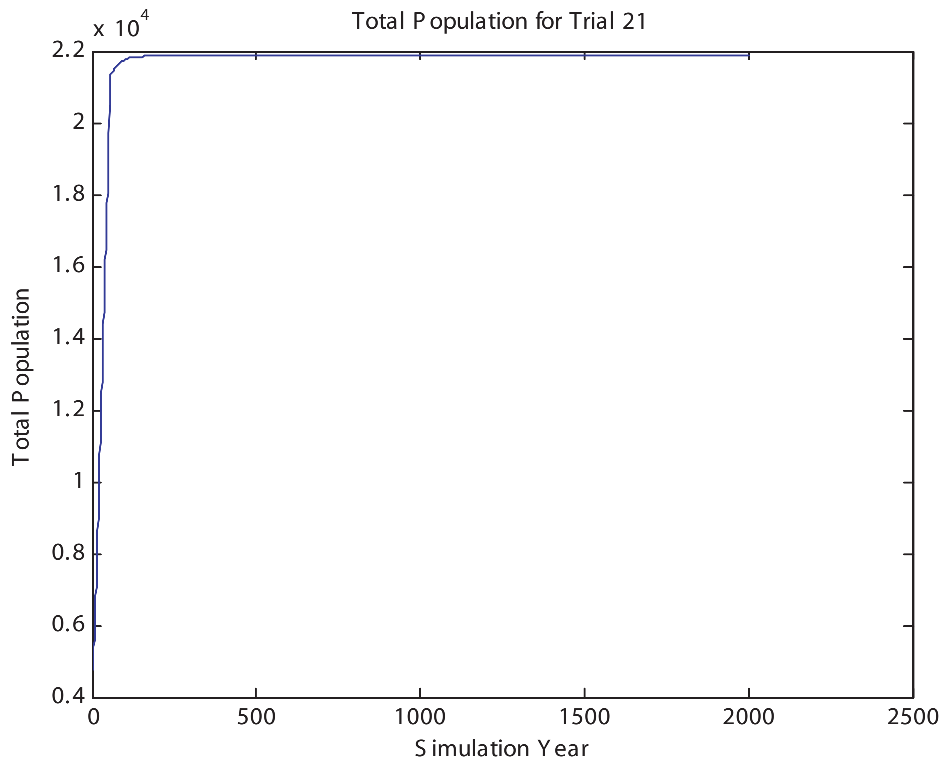

Figure 9b. Total Population, Unstable Environment, Trial 2

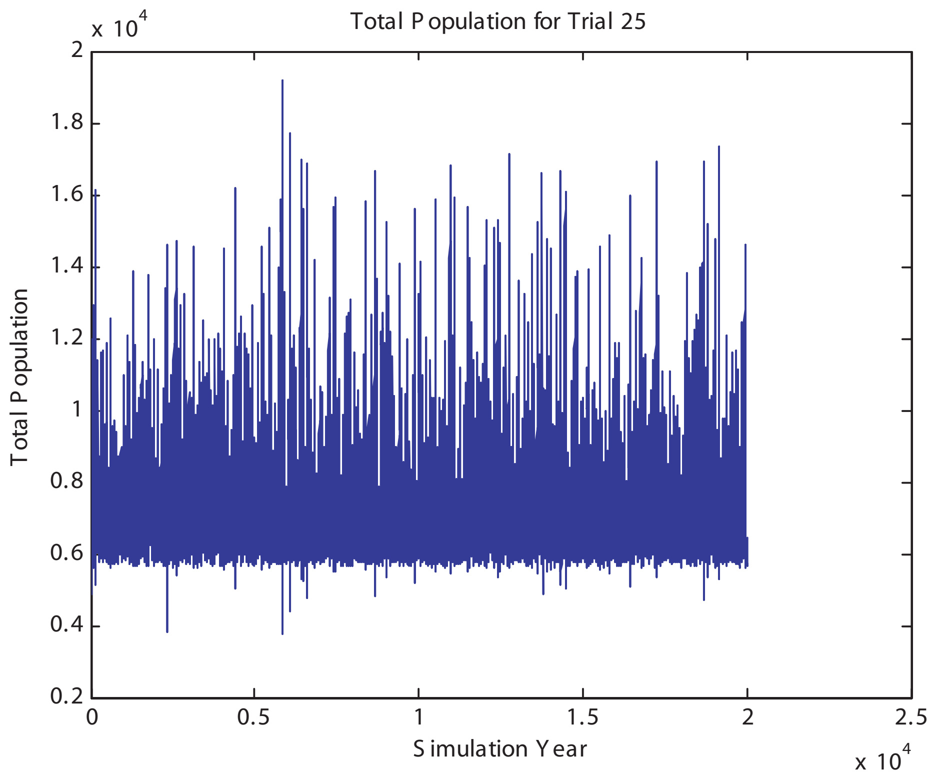

Figure 10a. Mean Group Population, Stable Environment, Trial 2

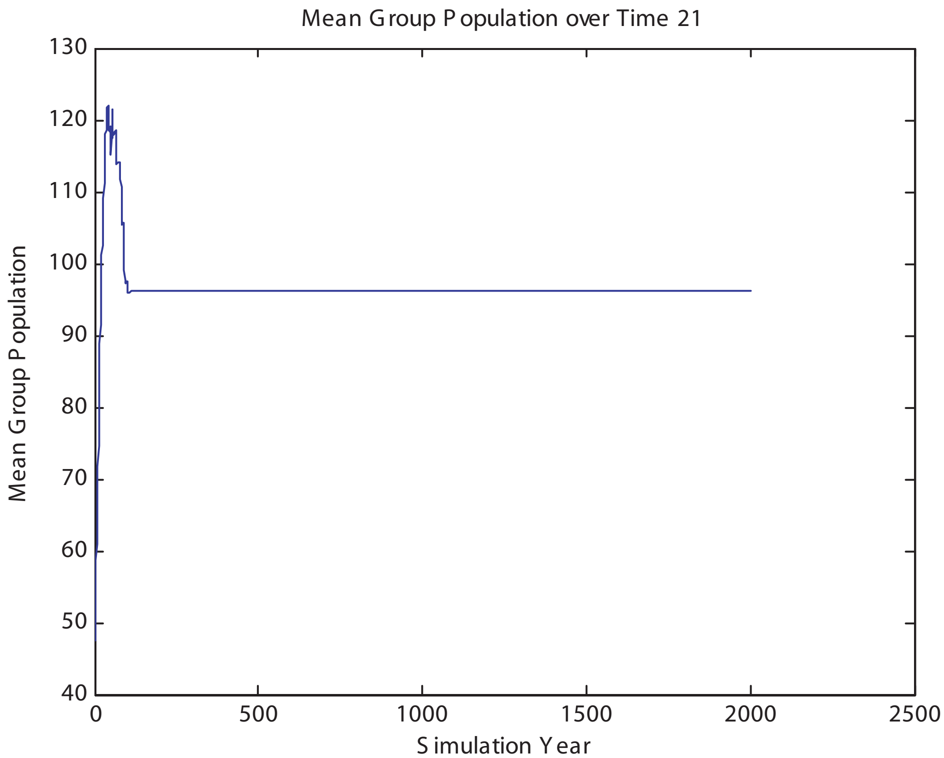

Figure 10b. Mean Group Population, Unstable Environment, Trial 2

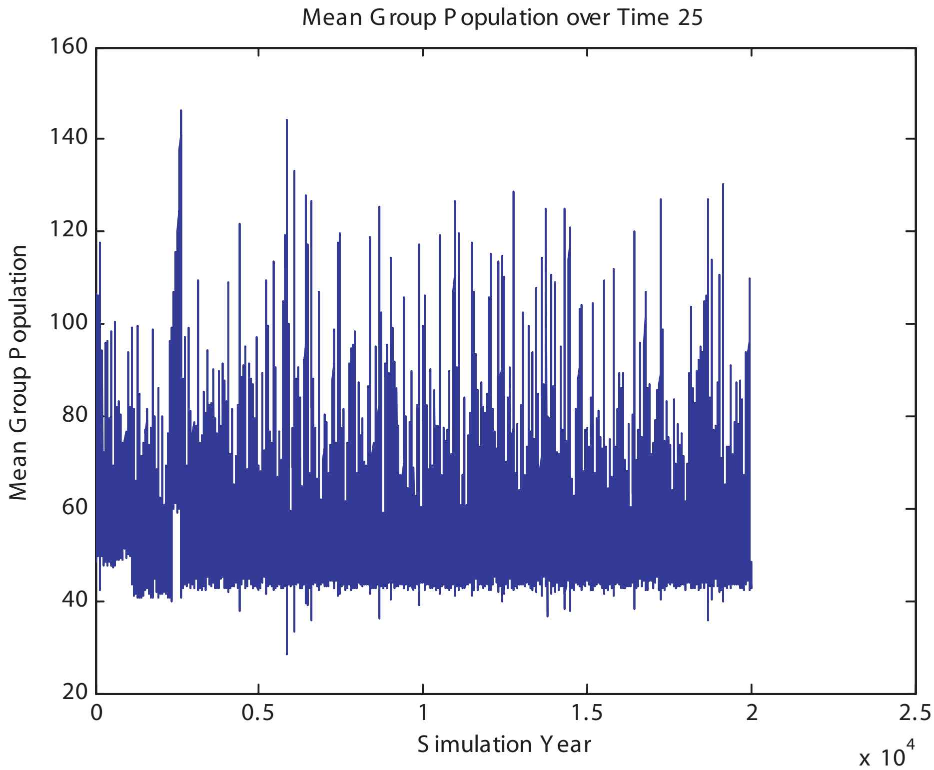

Figure 11a. Number of Extinctions, Stable Environment, Trial 2

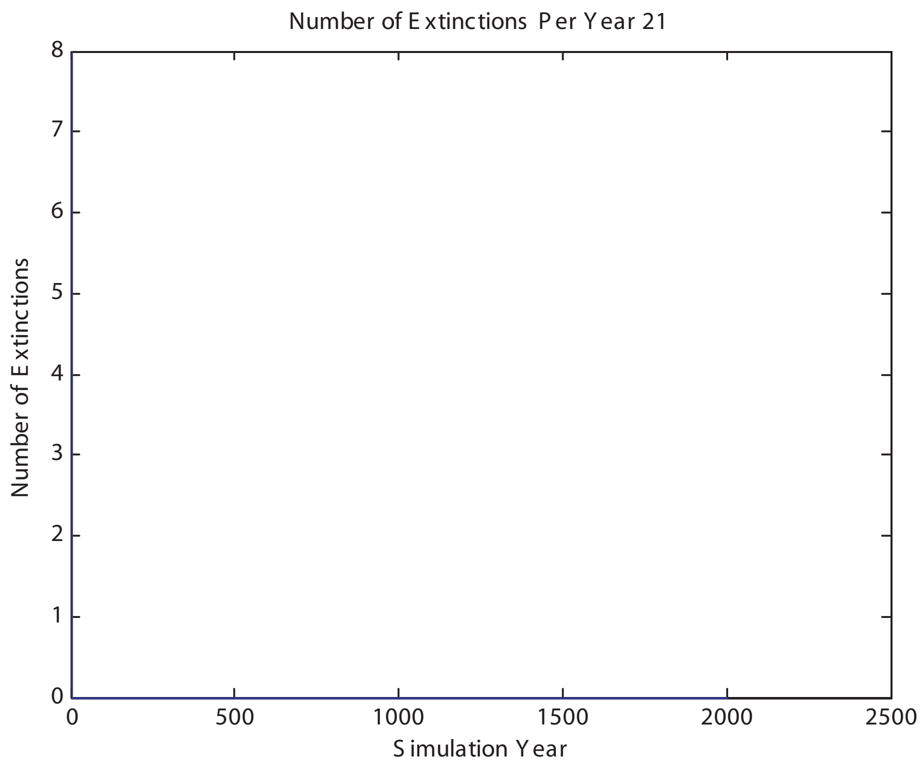

Figure 11b. Number of Extinctions, Unstable Environment, Trial 2

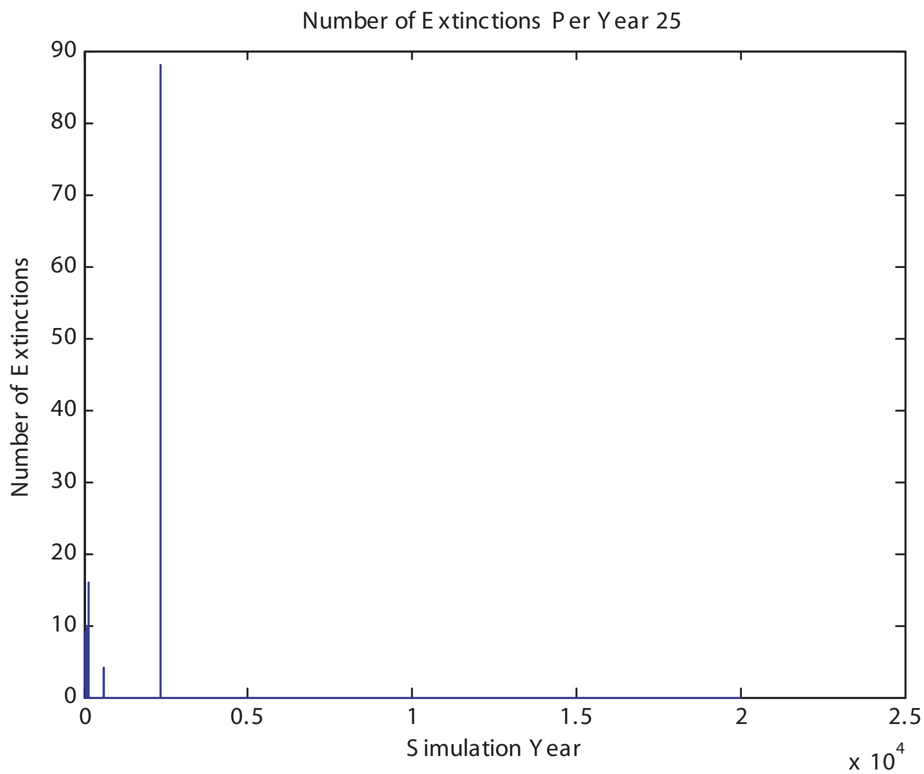

Figure 12a. Number of Splittings, Stable Environment, Trial 2

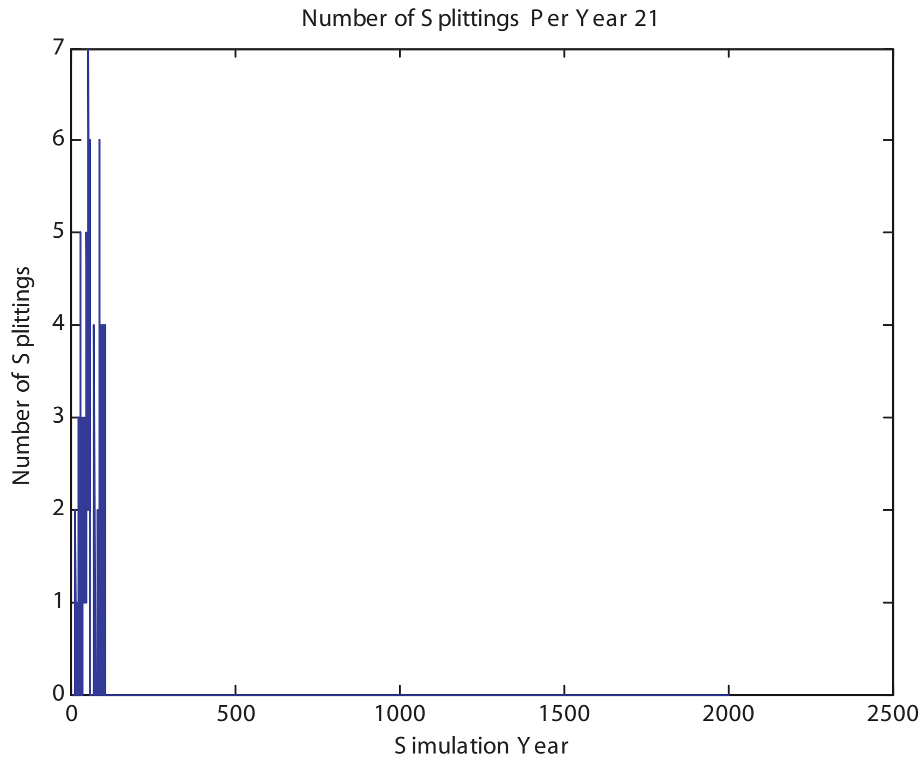

Figure 12b. Number of Splittings, Unstable Environment, Trial 2

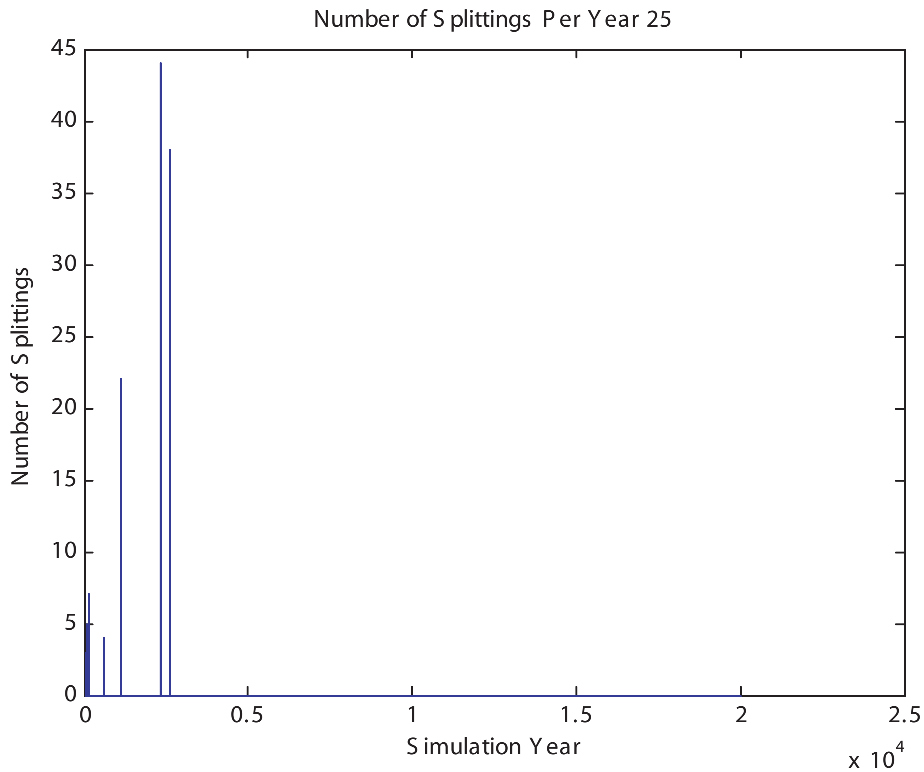

Figure 13a. Number of Groups, Stable Environment, Trial 2

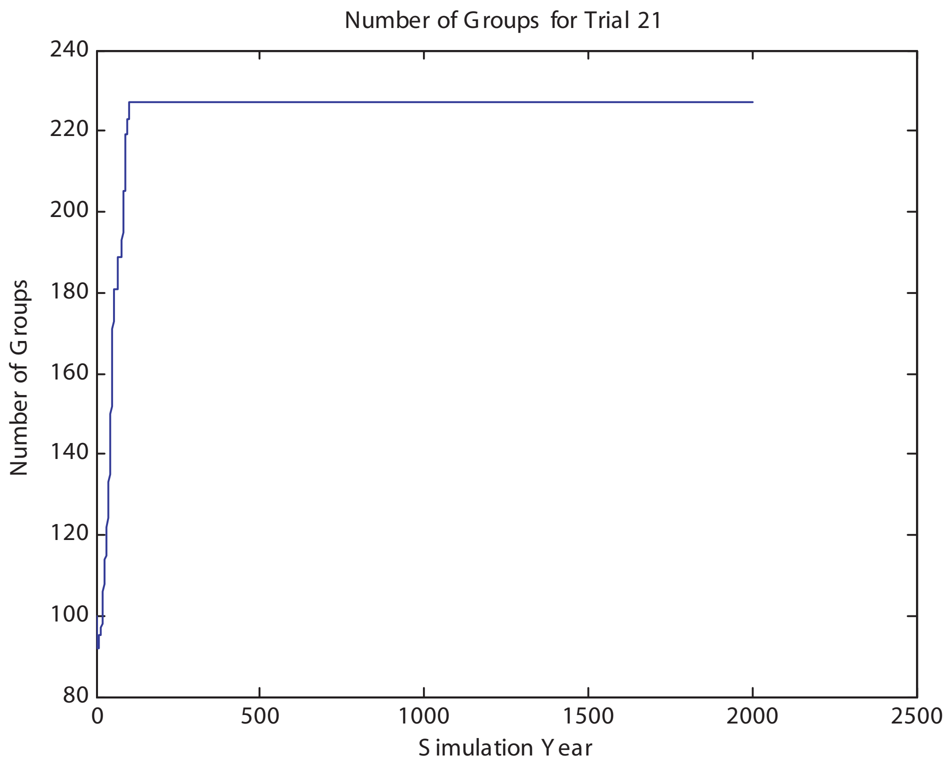

Figure 13b. Number of Groups, Unstable Environment, Trial 2

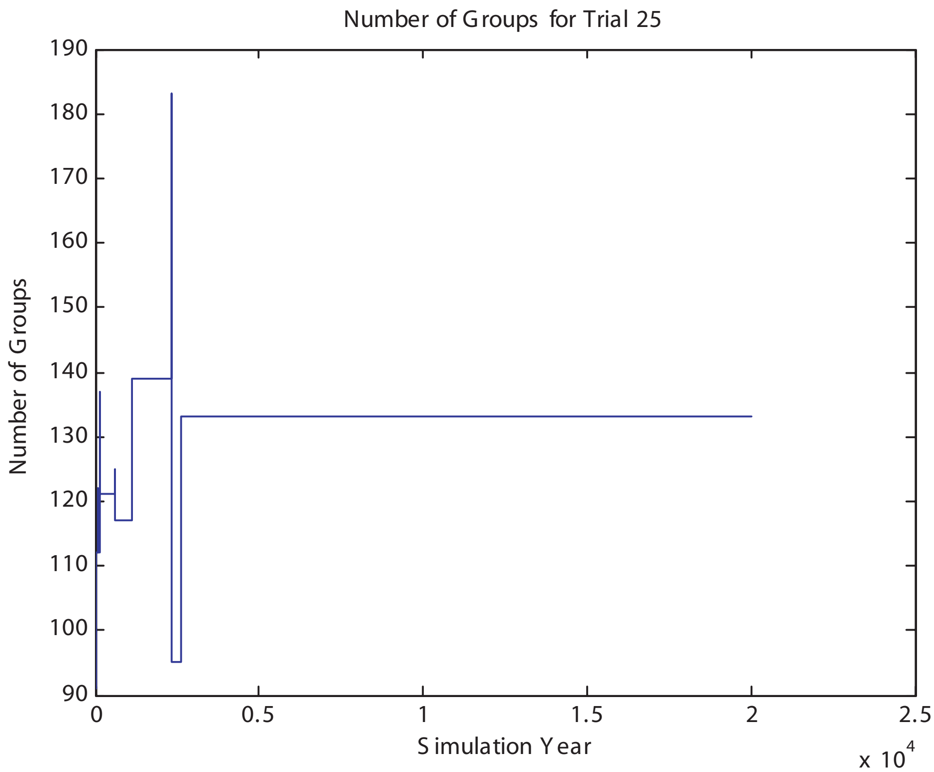

Figure 14a. Mean Upper Threshold Preference, Stable Environment, Trial 2

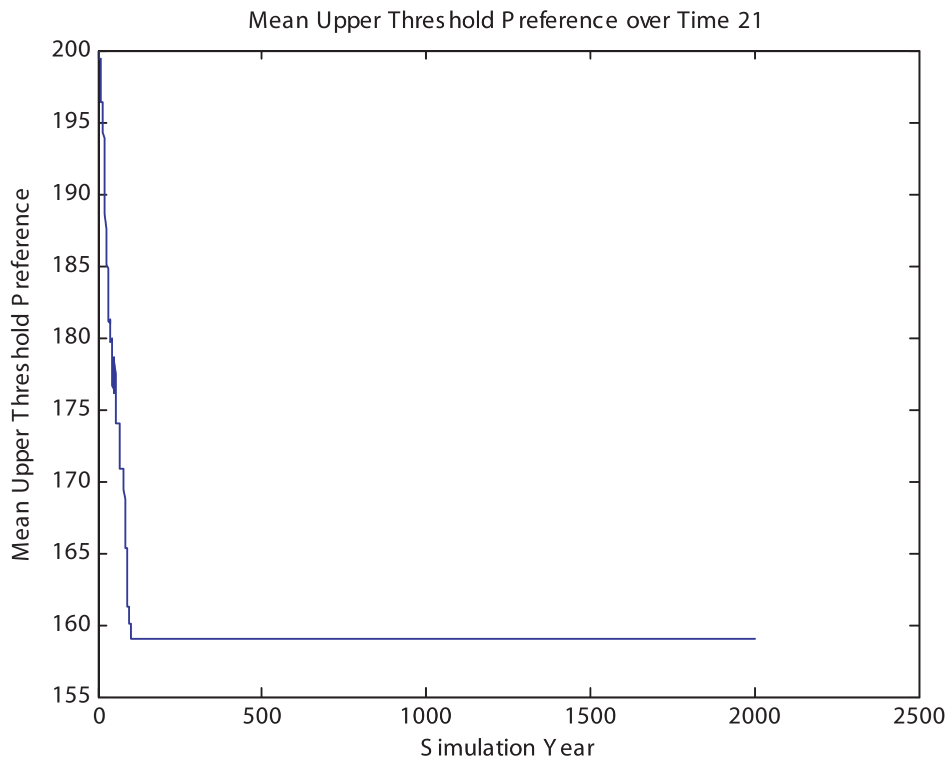

Figure 14b. Mean Upper Threshold Preference, Unstable Environment, Trial 2

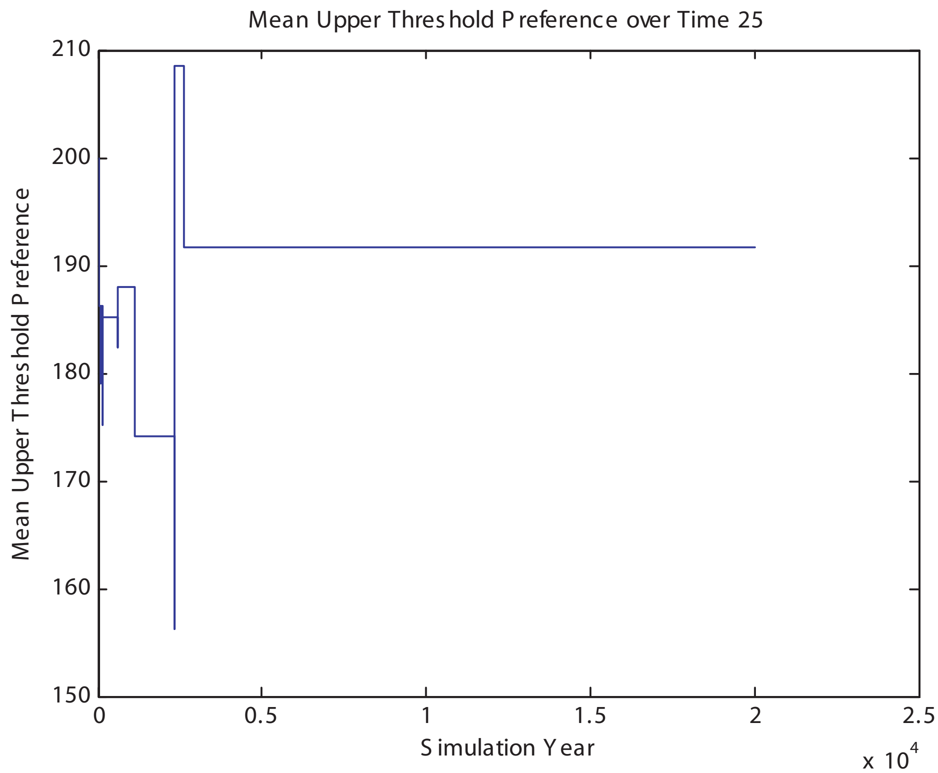

Figure 15a. Weighted Mean Upper Threshold Preference, Stable Environment, Trial 2

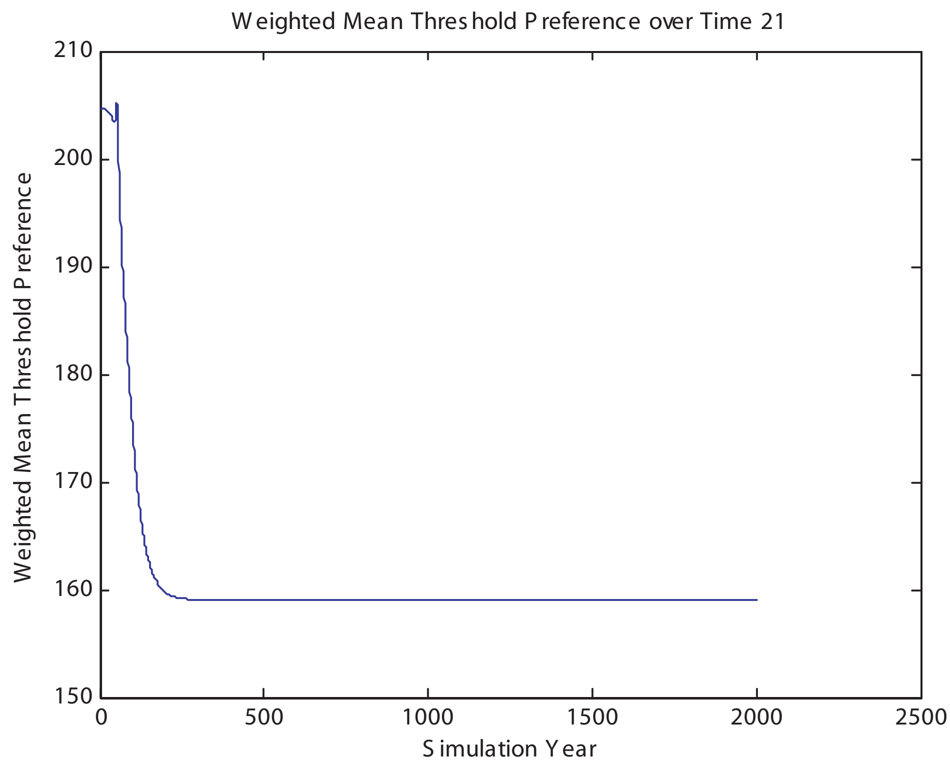

Figure 15b. Weighted Mean Upper Threshold Preference, Unstable Environment, Trial 2

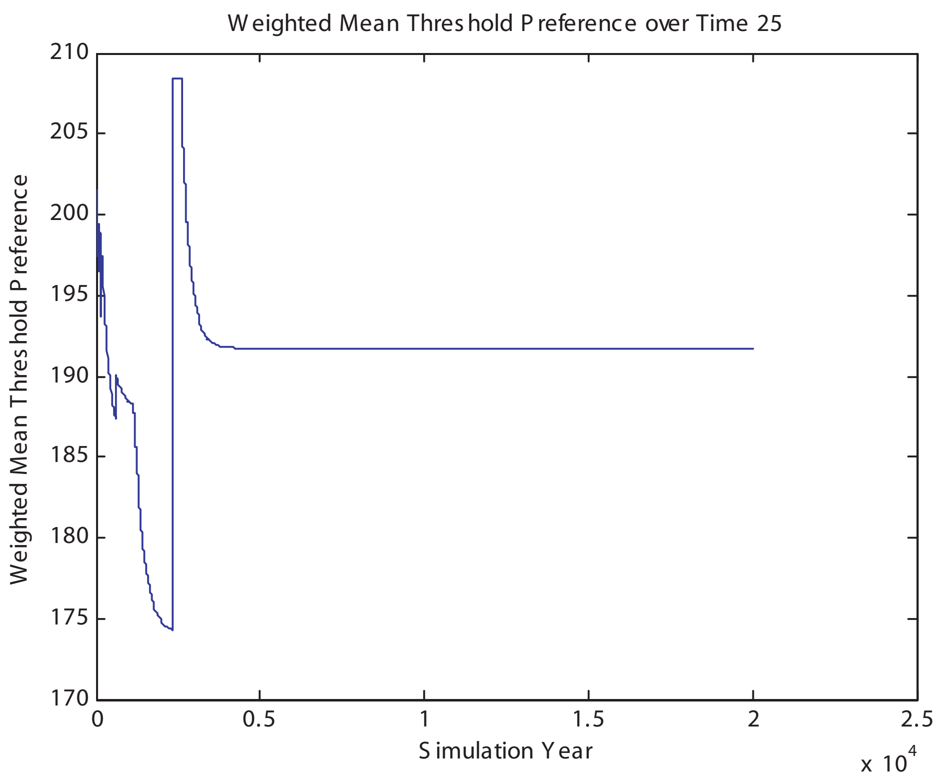

Figure 16a. Total Population, Stable Environment, Trial 3

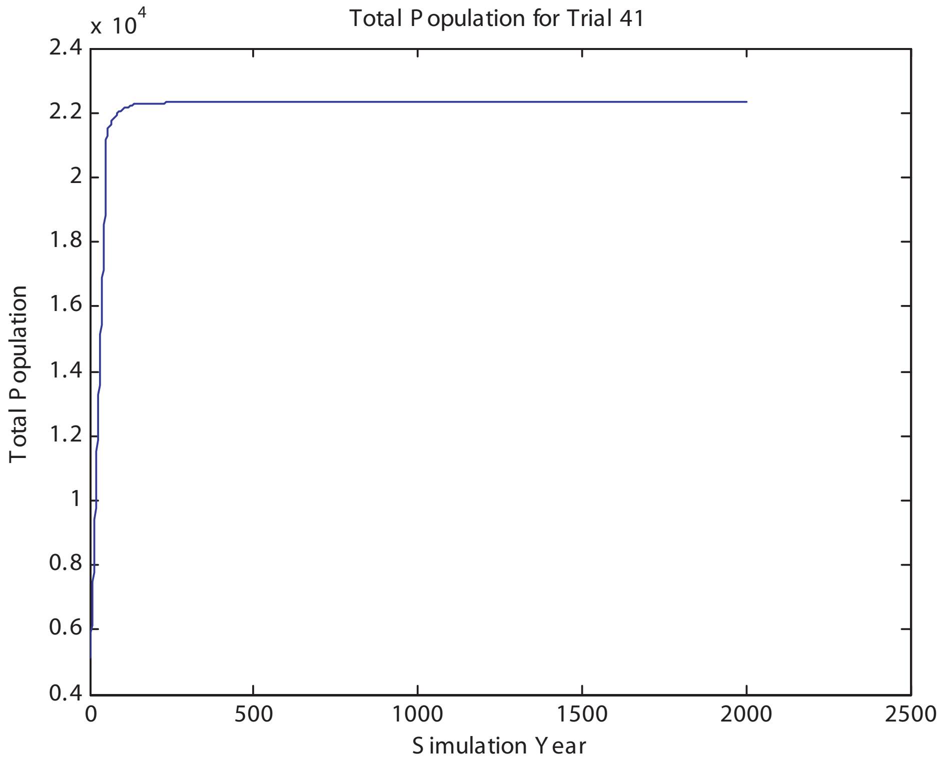

Figure 16b. Total Population, Unstable Environment, Trial 3

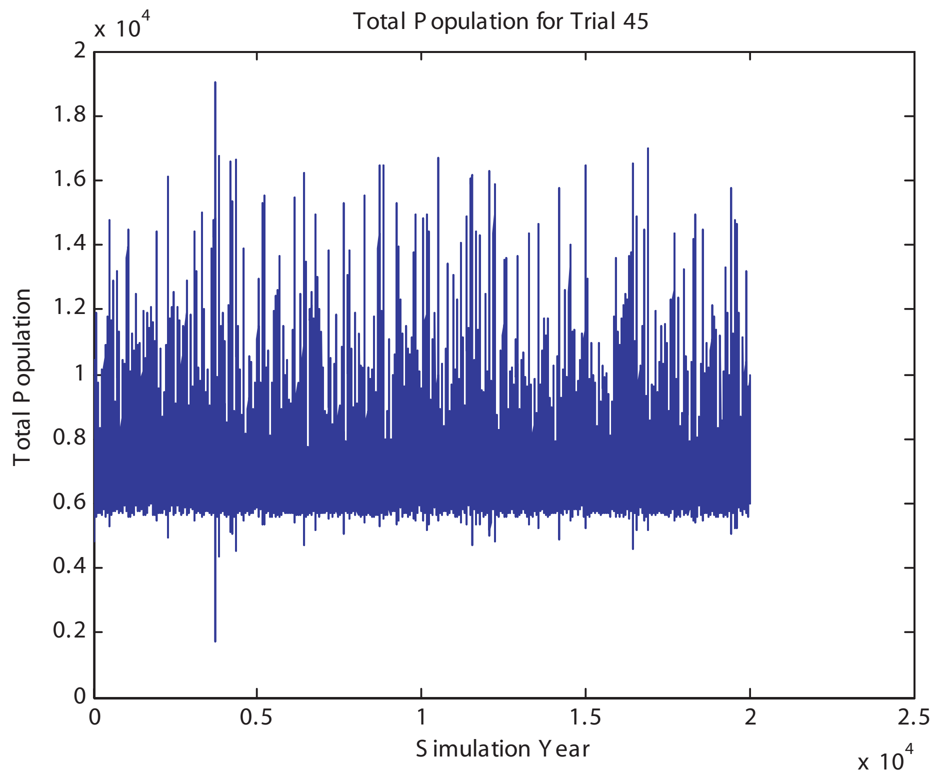

Figure 17a. Mean Group Population, Stable Environment, Trial 3

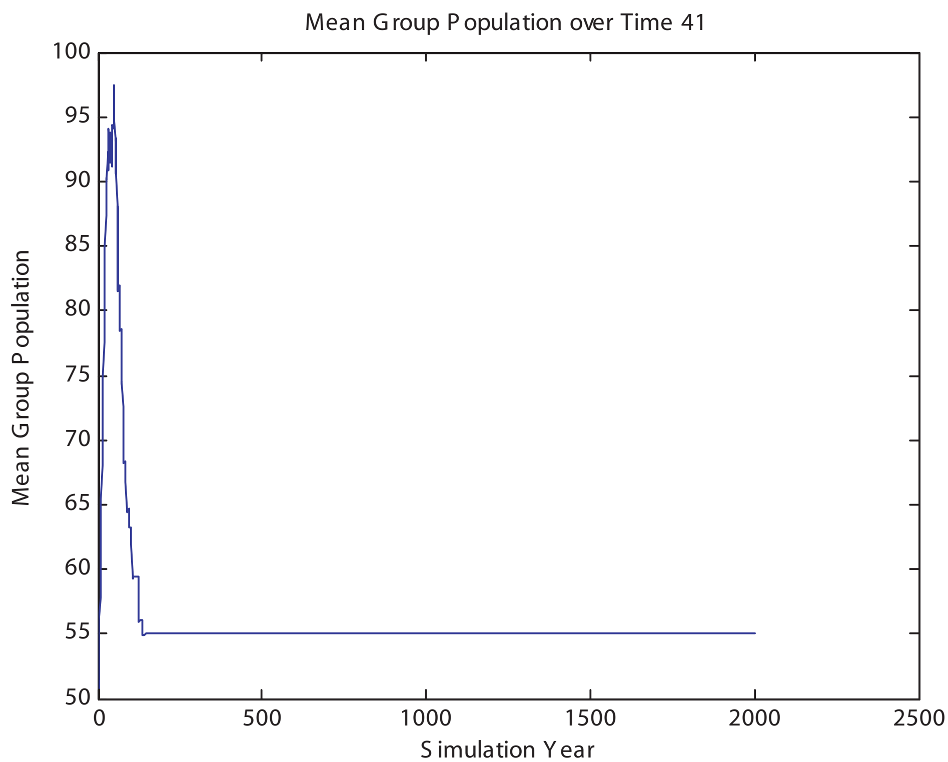

Figure 17b. Mean Group Population, Unstable Environment, Trial 3

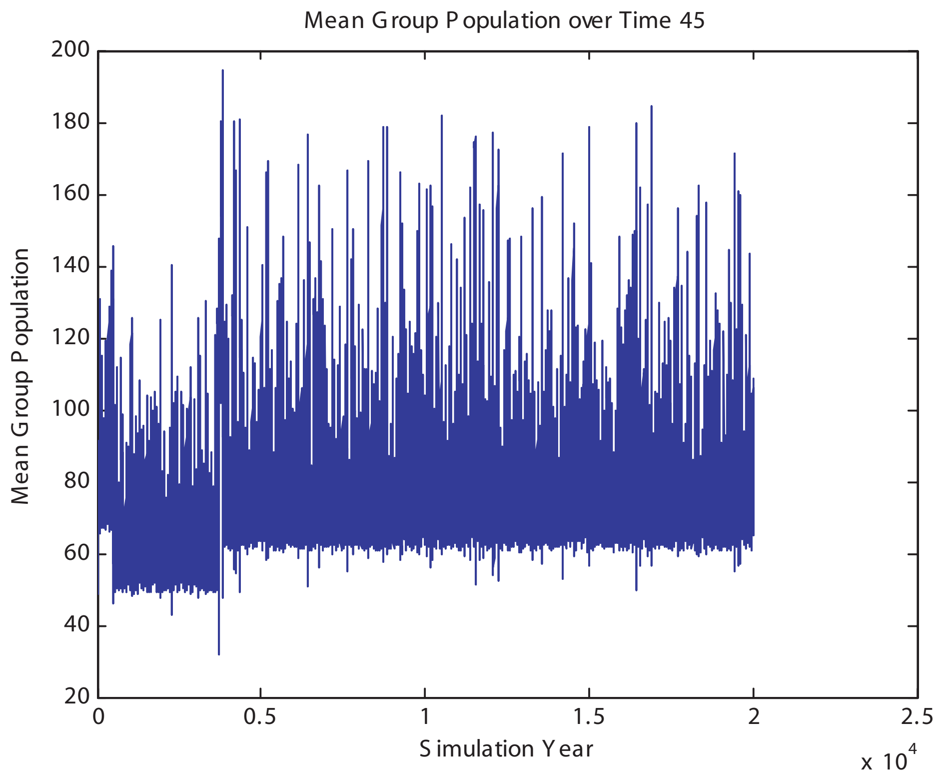

Figure 18a. Number of Extinctions, Stable Environment, Trial 3

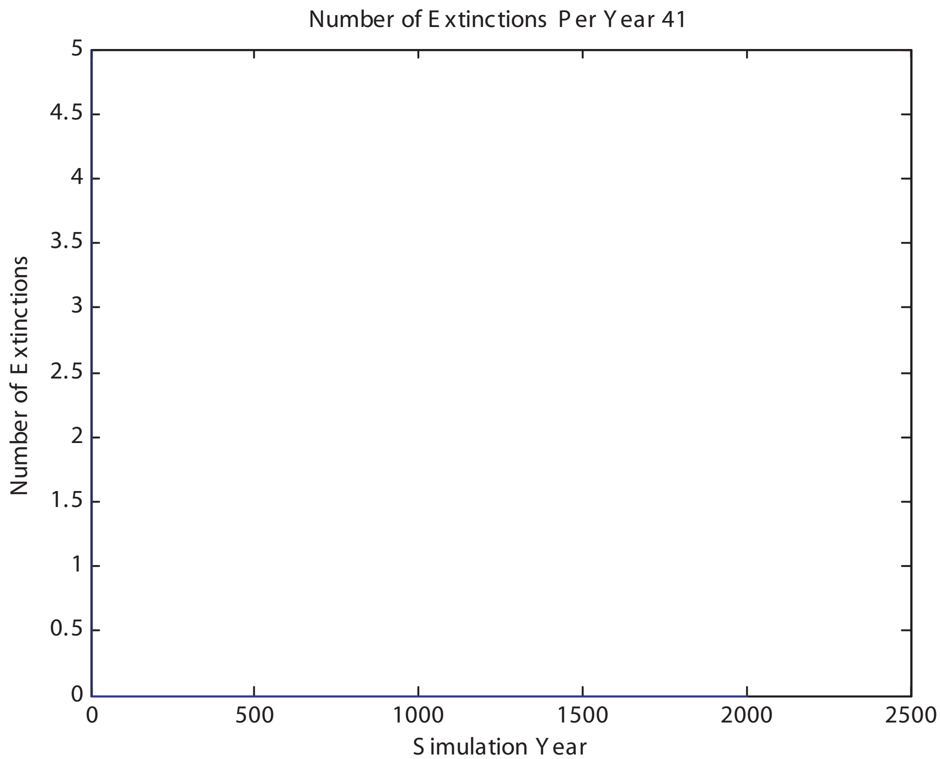

Figure 18b. Number of Extinctions, Unstable Environment, Trial 3

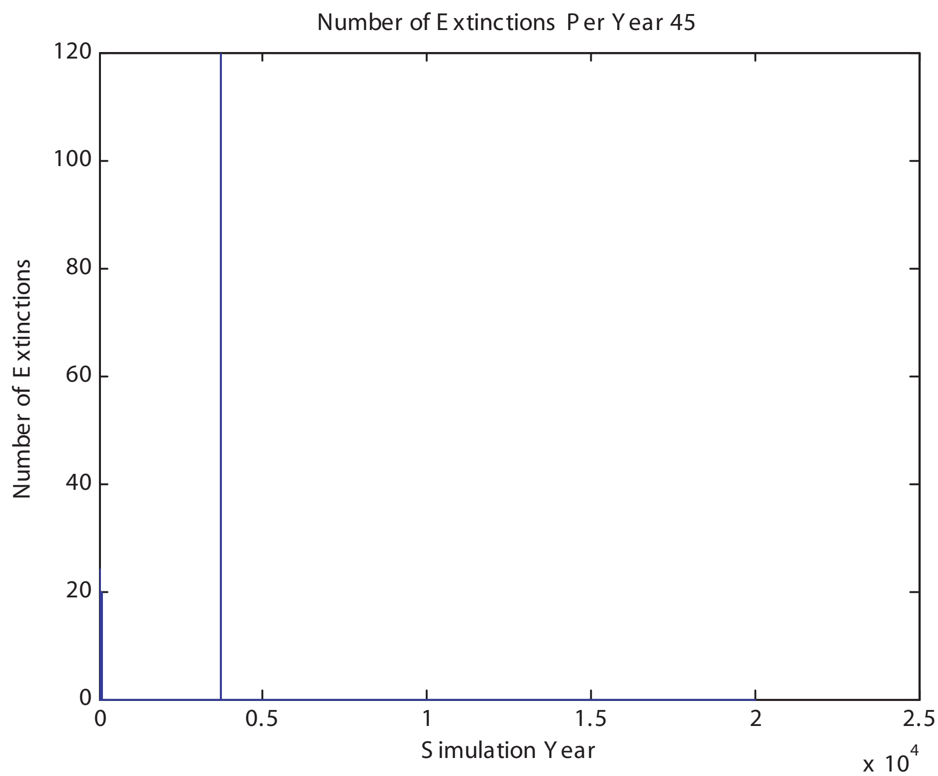

Figure 19a. Number of Splittings, Stable Environment, Trial 3

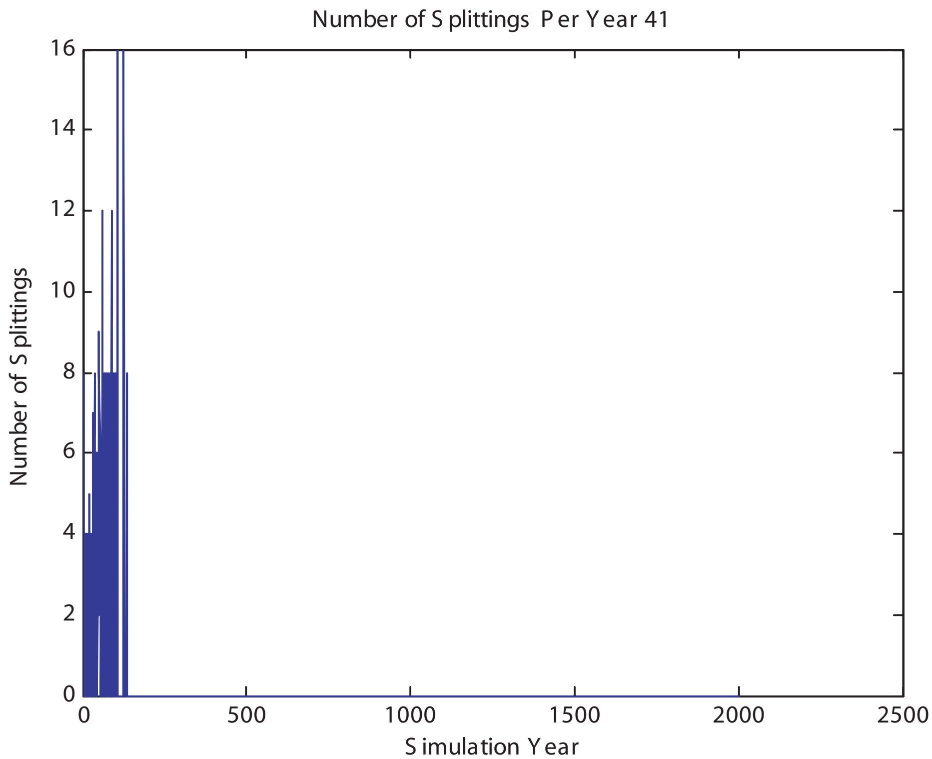

Figure 19b. Number of Splittings, Unstable Environment, Trial 3

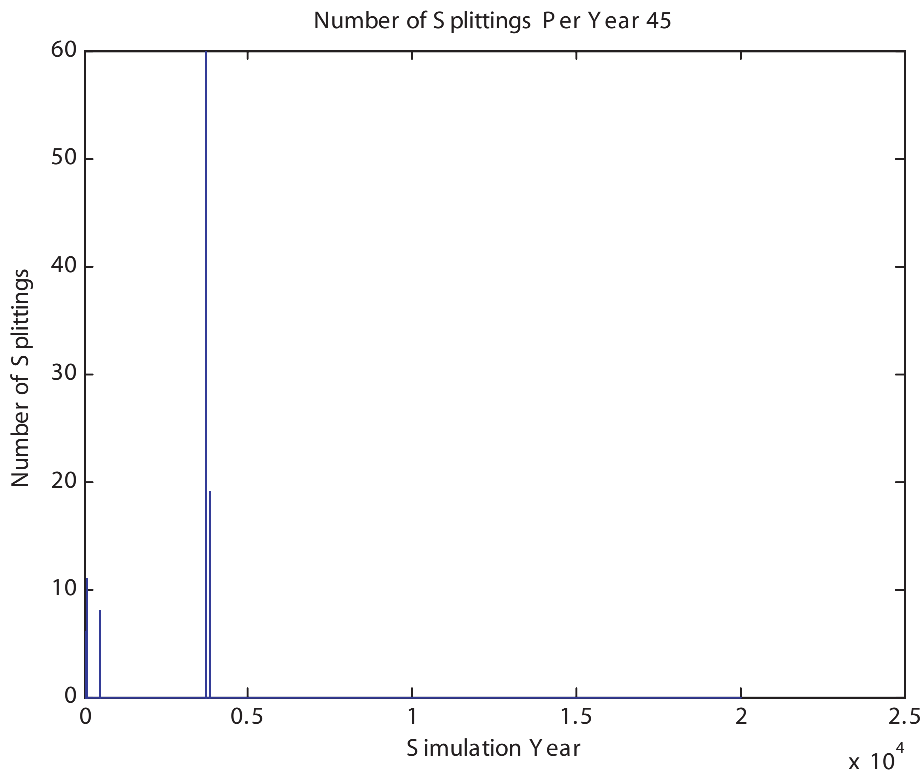

Figure 20a. Number of Groups, Stable Environment, Trial 3

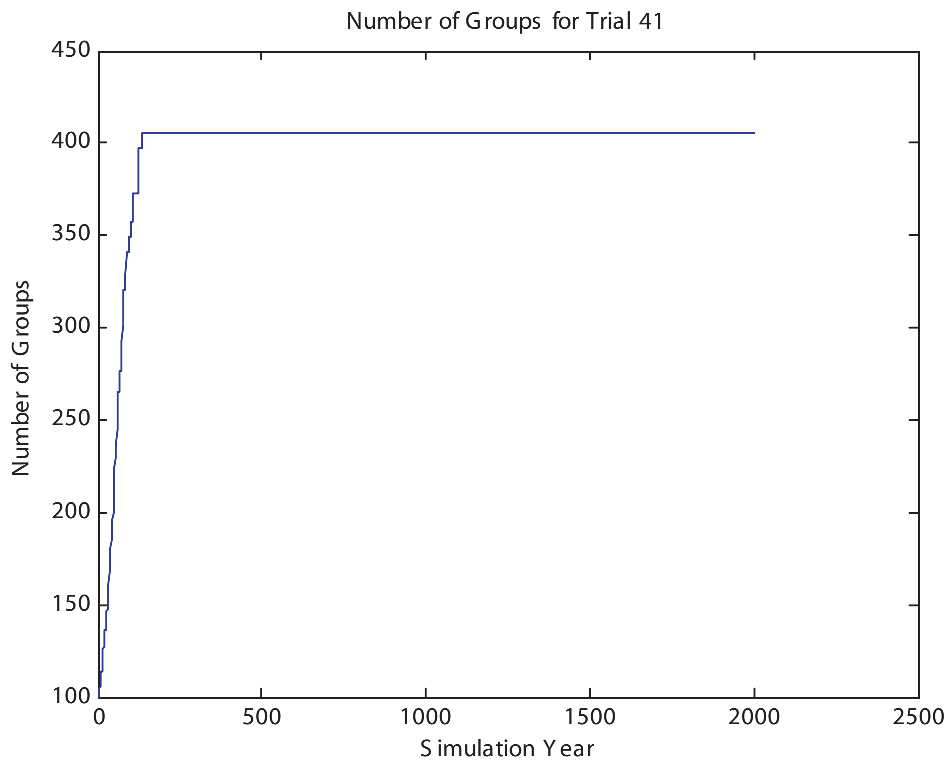

Figure 20b. Number of Groups, Unstable Environment, Trial 3

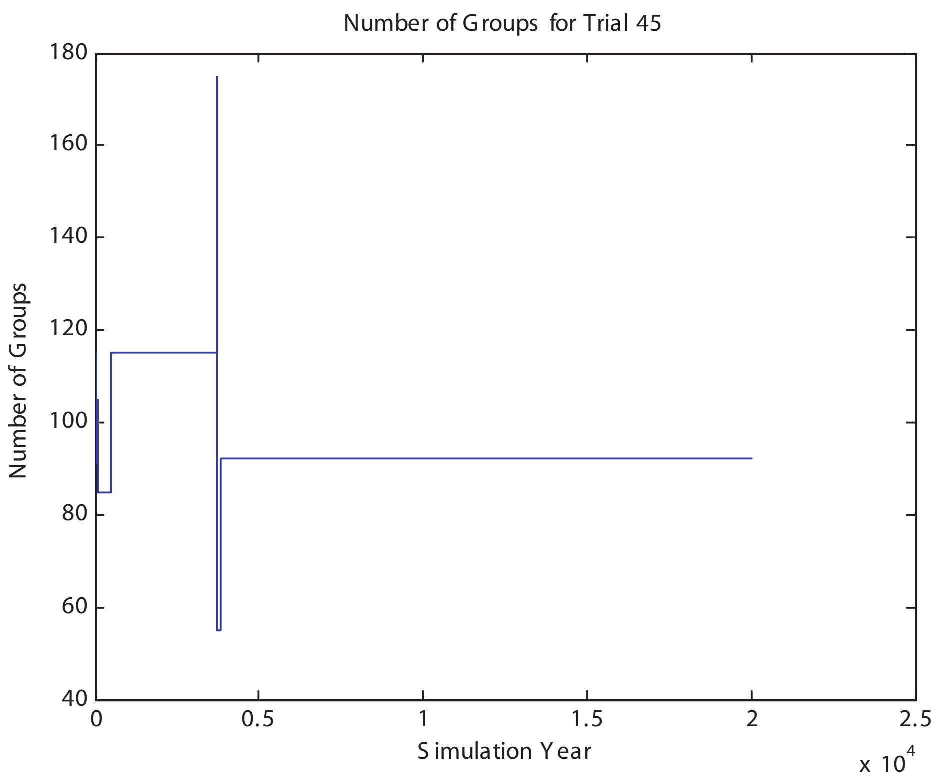

Figure 21a. Mean Upper Threshold Preference, Stable Environment, Trial 3

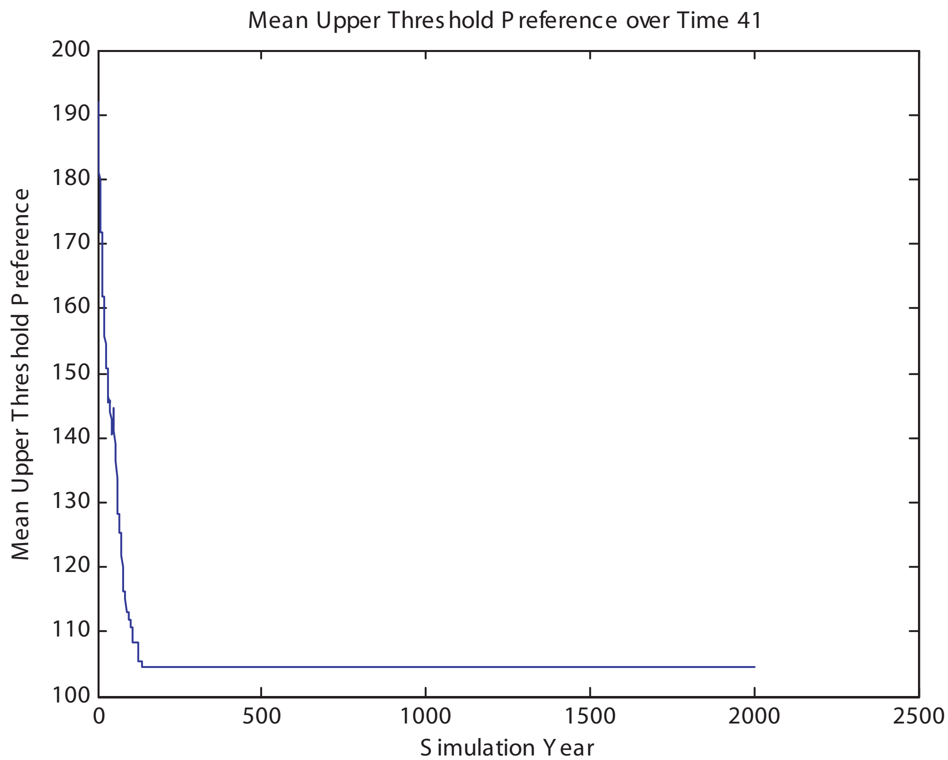

Figure 21b. Mean Upper Threshold Preference, Unstable Environment, Trial 3

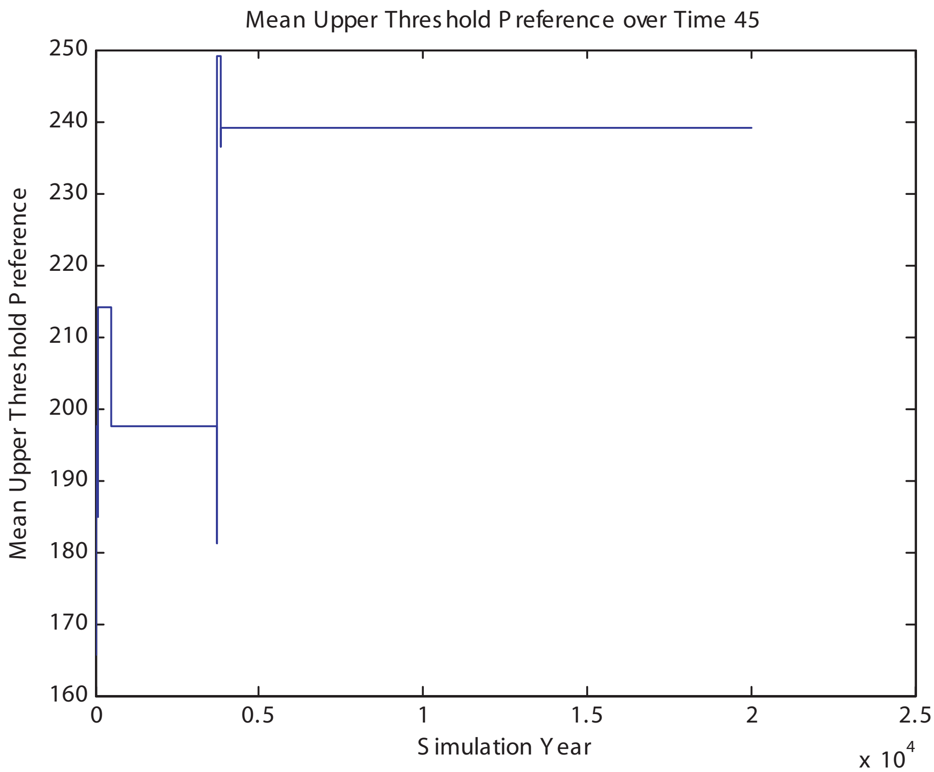

Figure 22a. Weighted Mean Upper Threshold Preference, Stable Environment, Trial 3

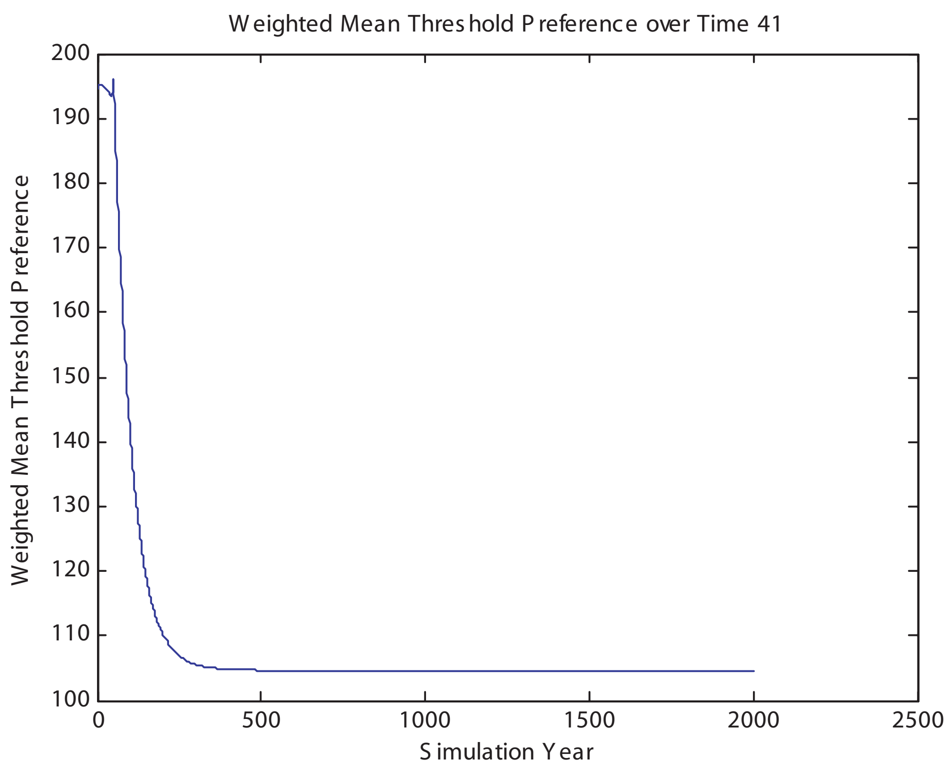

Figure 22b. Weighted Mean Upper Threshold Preference, Unstable Environment, Trial 3

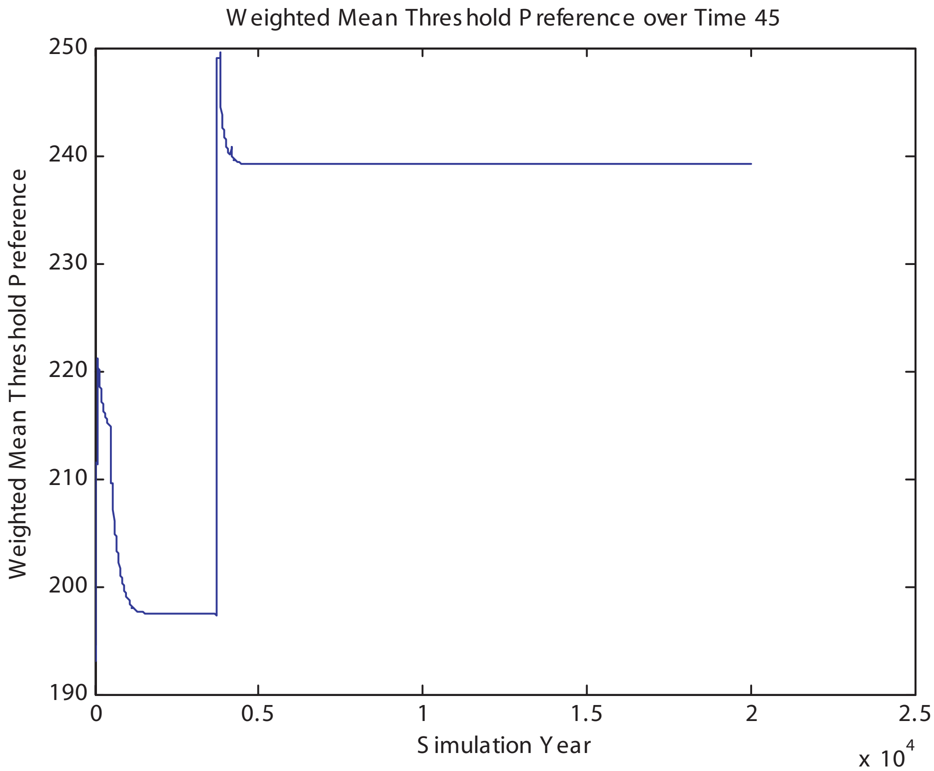

Figure 23a. Total Population, Stable Environment, Trial 4

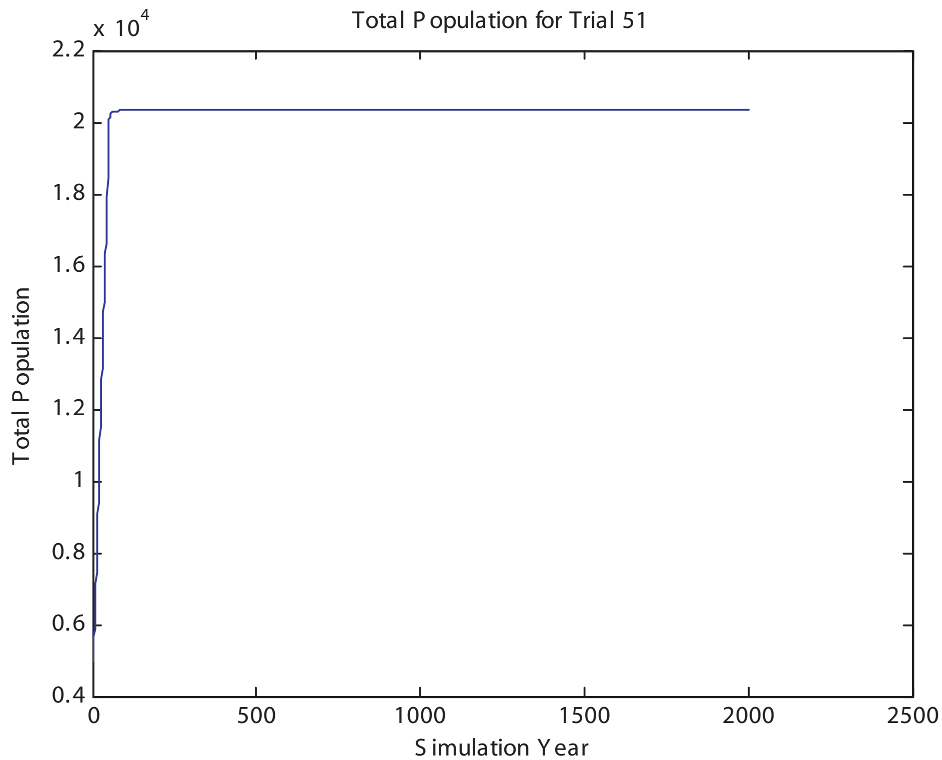

Figure 23b. Total Population, Unstable Environment, Trial 4

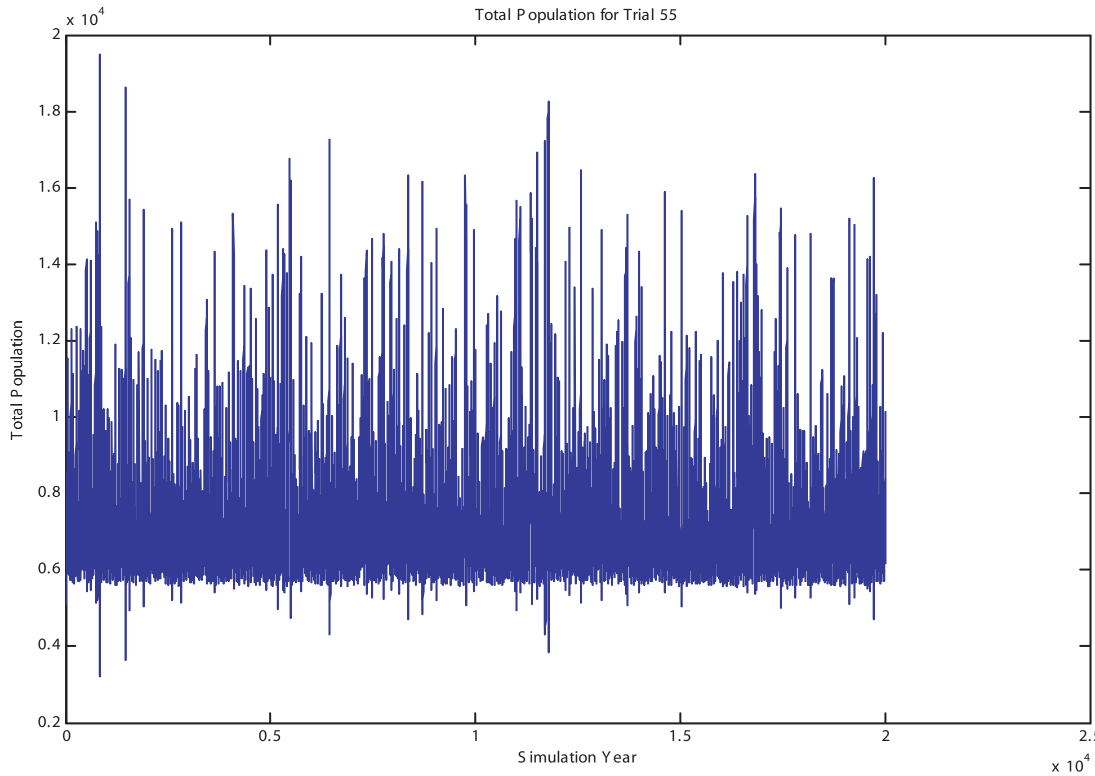

Figure 24a. Mean Group Population, Stable Environment, Trial 4

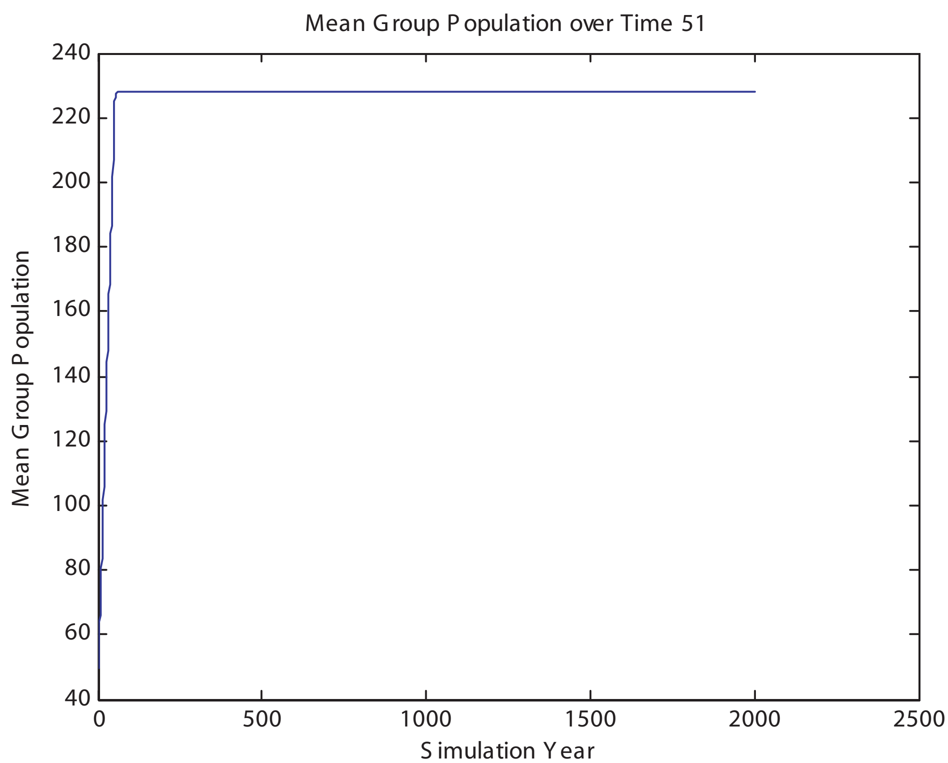

Figure 24b. Mean Group Population, Unstable Environment, Trial 4

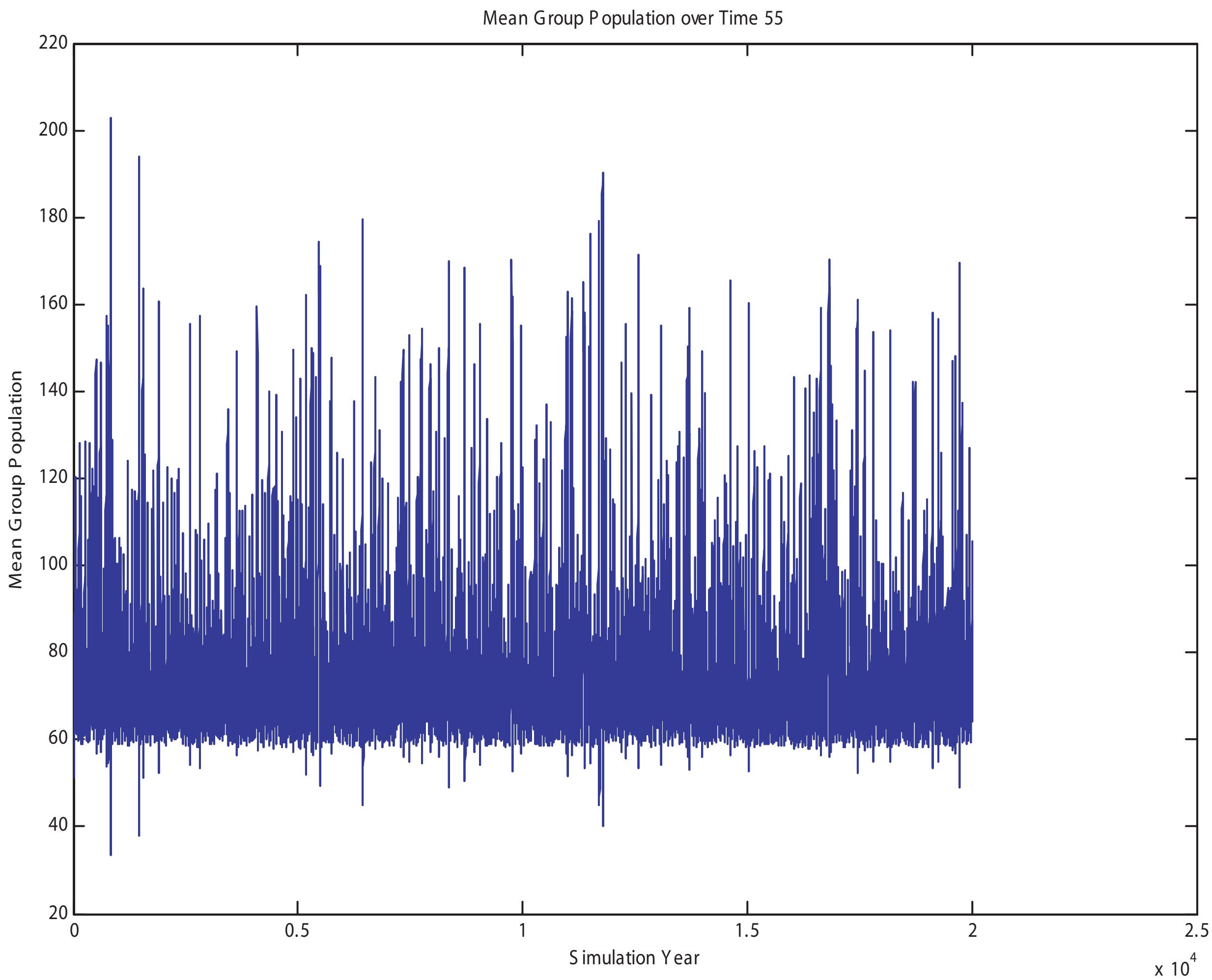

Figure 25a. Number of Extinctions, Stable Environment, Trial 4

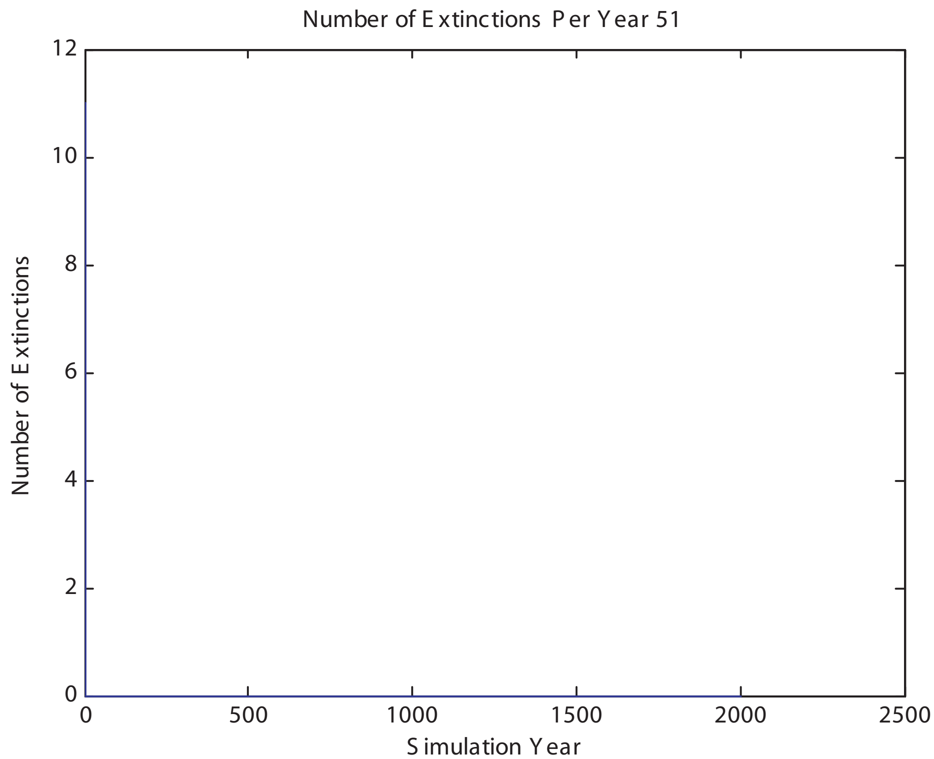

Figure 25b. Number of Extinctions, Unstable Environment, Trial 4

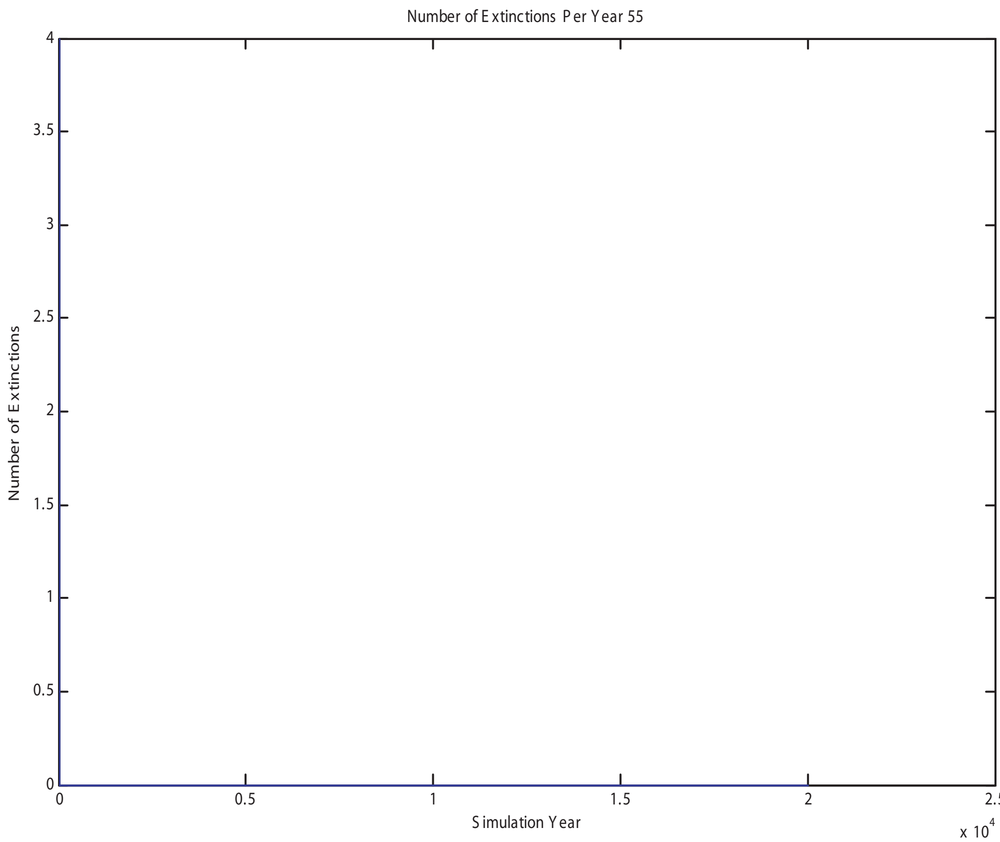

Figure 26a. Number of Splittings, Stable Environment, Trial 4

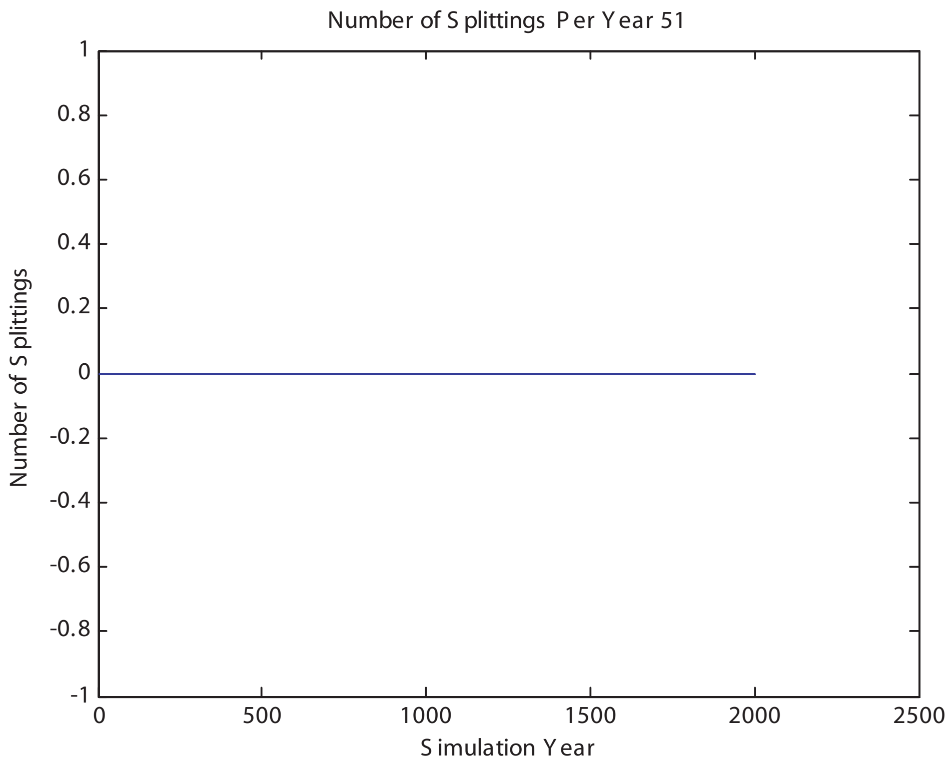

Figure 26b. Number of Splittings, Unstable Environment, Trial 4

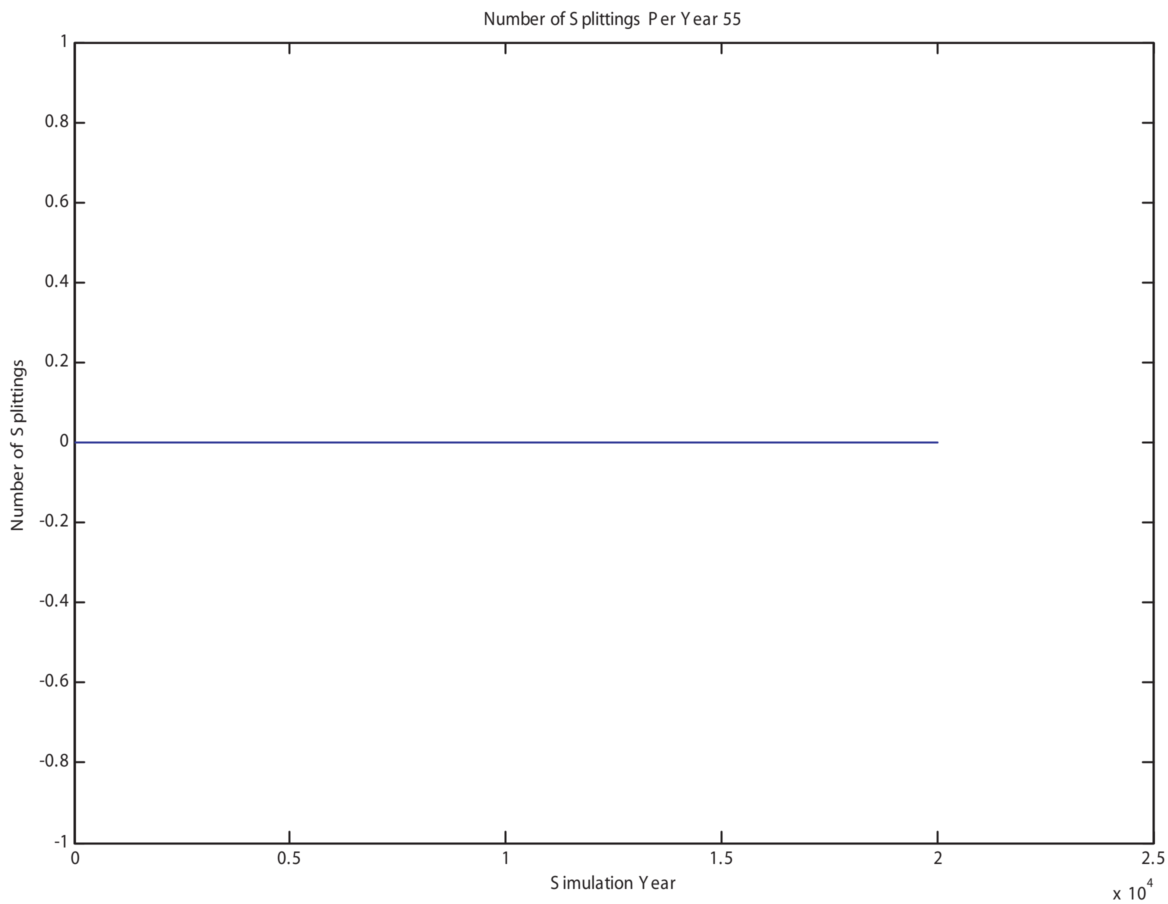

Figure 27a. Number of Groups, Stable Environment, Trial 4

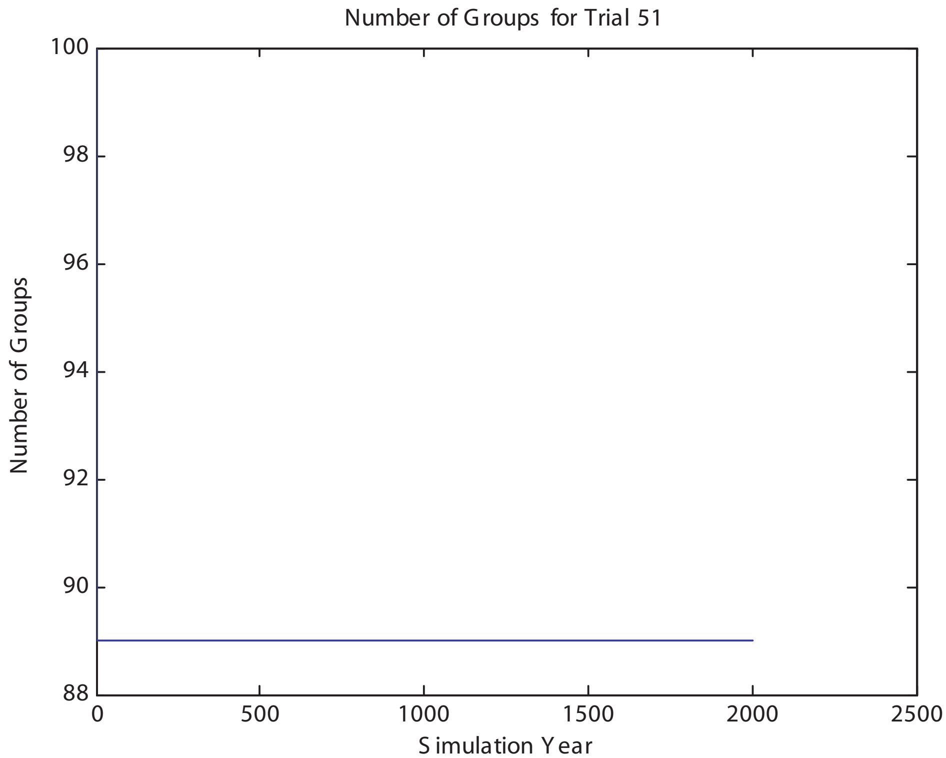

Figure 27b. Number of Groups, Unstable Environment, Trial 4