

Rules of thumb for metapopulation management

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Abstract: Many species live in ecosystems where resources are distributed patchily within the landscape. Furthermore, an ever-increasing number of species are forced to live in fragmented landscapes due to the destruction of their habitat, generally caused by anthropogenic disturbance. These metapopulations are consequently drawing much attention in both the theoretical and applied ecology literature (Levins (1969), Gilpin and Hanski (1991), Hanski (1999) and Dobson (2003)).

Habitat fragmentation caused by habitat loss, in combination with other factors such as climate change, is placing many species at high risk of extinction, and ecologists and conservation biologists must attempt to limit this risk. With less funding than is required to protect all species, triage becomes necessary, and hence the need to efficiently evaluate extinction risk in order to determine a priority for allocating funding (Hobbs and Kristjanson (2003)). Additionally, in order to use the resources available most efficiently, it is necessary to determine the optimal investment that minimises the threat of extinction.

We present here two 'rules of thumb' for metapopulation management, which are established using a simple metapopulation model. The first rule [R1] identifies an explicit formula for the persistence time of the population, and thus enables the population manager to form a priority species ranking by identifying those species most at risk of extinction. The second rule [R2] identifies an optimal management strategy that gives direction on how to alter the colonisation rate c (creation or improvement of habitat corridors) and local extinction rate e (restoring habitat quality or expanding habitat) in order to maximise the persistence time under a budgetary constraint.

We employ a stochastic version of the Levins (1969) metapopulation model. In order to use our rules of thumb it is necessary that this simple model first be *calibrated* to a spatially-realistic model. Thus we propose an explicit method for calibration for a general spatially-realistic model.

Rule [R1] is based on exact and approximate formulae for the expected time to extinction starting from a given initial number of occupied patches. Rule [R2] defines an optimal management strategy in terms of a total budget B and costs K_c and K_e for respective (per unit) changes in c and e :

Invest in reducing e to its allowable minimum, unless $B < K_e e - K_c c$, in which case invest in increasing c .

We conclude by testing our rules on computer-generated patch networks from a spatially-realistic metapopulation model and a model for malleefowl (*Leipoa ocellata*) in the Bakara region of South Australia. These results suggest that our rules of thumb, derived from the stochastic Levins model, are robust. This, as well as optimal methods based on approximations for other spatially-realistic models, will be explored fully elsewhere.

Keywords: Costs; metapopulations; management; rules of thumb; spatially-realistic; stochasticity

1. INTRODUCTION

The metapopulation paradigm has proved to be useful for studying species dynamics; many species exist naturally in a network of geographically separated patches, and many others have suffered modification of habitat, generally due to anthropogenic disturbance, resulting in their occupying a mosaic of patches (Levins (1969), Gilpin and Hanski (1991), Hanski (1999) and Dobson (2003)). Such habitat fragmentation, in combination with other factors such as climate change, is placing species at high risk of extinction. Ecologists and conservation biologists must attempt to limit this risk. With less funding than is required to protect all species, they must rank extinction risk in order to determine priority in allocating funding (Hobbs and Kristjanson (2003)), and determine the optimal way to invest available funding to minimise extinction threat.

This paper provides ‘rules of thumb’ for ranking metapopulation extinction risk, allowing a rapid evaluation of species priority rankings, and for determining optimal management strategies under constrained conservation funding. Their best feature is simplicity; the formulae can be evaluated quickly, yet they are sufficiently accurate to be of benefit to the conservation community. We investigate this accuracy by testing our rules on computer-generated patch networks for a spatially-realistic metapopulation model, and data for an Australian species of concern to conservationists.

2. RULES OF THUMB

We will use a stochastic formulation of the classical Verhulst (1838) model for population growth, which first appeared in the metapopulation context in the much-cited paper of Levins (1969). There are N patches, which are always suitable for occupancy. Propagules (individuals) emanate from each occupied patch (and survive to reach another patch) at rate c (commonly called the *colonisation rate*) and each occupied patch becomes vacant (through extinction and migration) at rate e (commonly called the *local extinction rate*). If $n(t)$ denotes the number of occupied patches at time t , then $n'(t) = c(n/N)(N - n) - en$. Our stochastic formulation is a continuous-time Markov chain whose transition rates are given in Table 1. The spatially-realistic model we use as our gold-standard (for the purposes of this paper) models individual patch positions, affecting migration rate between patches, and patch areas, affecting the local extinction rate; the precise transition rates are given in Table 2.

Event	Transition from n to	Rate
Colonisation	$n + 1$	$c\frac{n}{N}(N - n)$
Extinction	$n - 1$	en

Table 1. Transition rates: simple model

Event	Transition from \mathbf{n} to	Rate
Colonisation	$\mathbf{n} + \mathbf{1}_i$	$g(1 - n_i) \sum_{j \neq i} n_j \exp(-\beta\sqrt{d_{ij}})$
Extinction	$\mathbf{n} - \mathbf{1}_i$	$\kappa n_i / A_i$

Table 2. Transition rates: spatially-realistic model

In our spatially-realistic model the state is $\mathbf{n} = (n_1, n_2, \dots, n_N)$, where the i th entry equals 1 if patch i is occupied, and 0 otherwise, $\mathbf{1}_i$ is used to denote a vector with a 1 in the i th entry and 0s elsewhere, g is the base migration rate, β is the exponential dispersion parameter, d_{ij} is the distance between patches i and j , κ is the local extinction rate parameter, and A_i is the area of patch i . Thus we assume that the rate of colonisation decreases with distance between patches, and the rate of local extinction decreases with patch area.

Both models have absorbing states, corresponding to total extinction of the metapopulation, but if $c > e$ (for our simple model) the population settles down to a ‘quasi equilibrium’ that may persist for long periods (Pollett (2001)). The expected time to extinction is a frequently used measure of persistence, which we now evaluate for our simple model.

Species priority ranking [R1]. In the static landscape case the expected time to extinction starting from $n(0) = i$ occupied patches is

$$\tau_i = \frac{1}{e} \sum_{j=1}^i \sum_{k=0}^{N-j} \frac{1}{j+k} \prod_{l=0}^{k-1} \left(\frac{N-j-l}{N\rho} \right), \quad [\text{R1}]$$

where $\rho = e/c$. This may be evaluated rapidly. We also consider two approximations. The first is

$$\tau_i^{A1} = \frac{1}{c(1-\rho)} \left\{ E_\rho^N \left(\frac{1-\rho^i}{1-\rho} \right) \sqrt{\frac{2\pi}{N}} - \sum_{k=1}^{i-1} \frac{(1-\rho^{i-k})}{k} \right\}, \quad [\text{A1}]$$

where $\rho < 1$ and $E_\rho = e^{-(1-\rho)}/\rho$. Its accuracy improves as N increases, and reduces some computational expense, in particular if the initial number of occupied patches i is small. The second approximation is

$$\tau_i^{A2} = \frac{1}{c(1-\rho)} E_\rho^N \left(\frac{1-\rho^i}{1-\rho} \right) \sqrt{\frac{2\pi}{N}} - \frac{\gamma + \ln(i-1)}{c}, \quad [A2]$$

where γ is *Euler's constant*. The accuracy and robustness of the approximations is illustrated in Figure 1. We can see from (a) that populations of species most likely to be of conservation concern correspond to the black and dark-grey regions of the subplot: most concern black to least concern white. Plots (b) and (c), corresponding to approximations [A1] and [A2], respectively, show that both are reasonably accurate, with accuracy generally improving as both the number of patches N and the colonisation rate parameter c increase. Both approximations are highly accurate in those parts of the parameter space corresponding to species of limited conservation concern. In the rest of the parameter space they are sufficiently accurate to discern which species are of limited conservation concern, thus leaving only those requiring more precise evaluation of threat. We note that, with the exception of very small N and c , the approximations underestimate the expected time to extinction (a general feature) and thus provide a conservative assessment of risk.

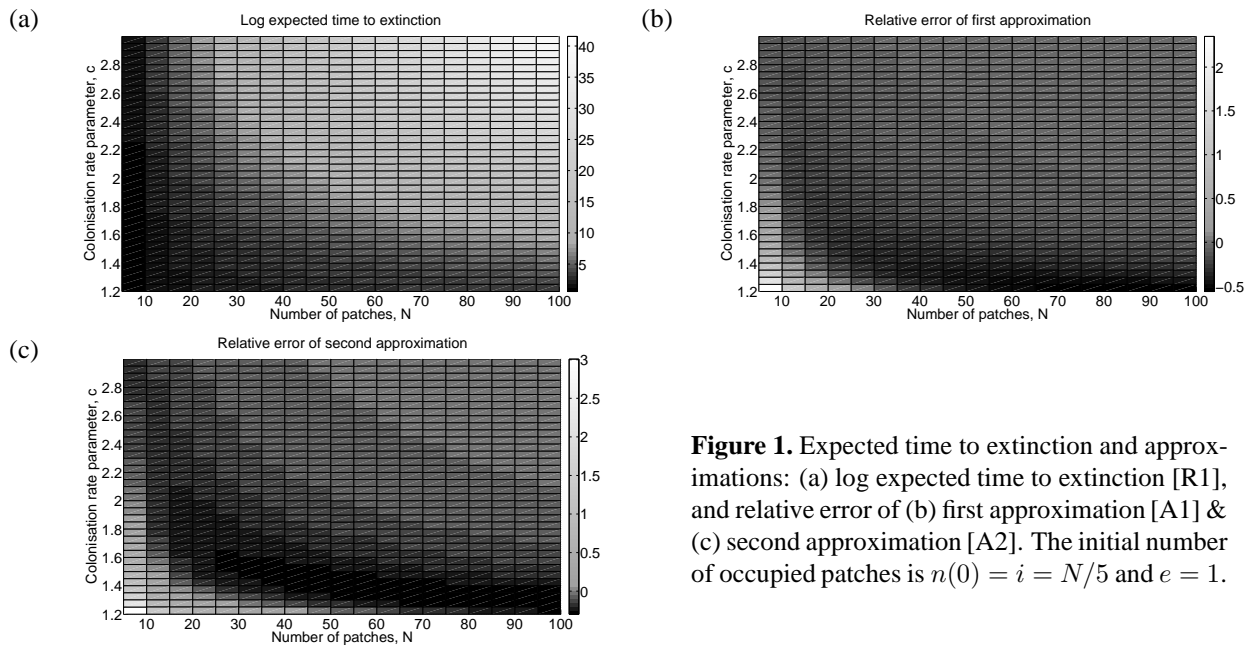


Figure 1. Expected time to extinction and approximations: (a) log expected time to extinction [R1], and relative error of (b) first approximation [A1] & (c) second approximation [A2]. The initial number of occupied patches is $n(0) = i = N/5$ and $e = 1$.

Formulae [R1] forms our first rule of thumb; comparison of [R1] for different species, having different colonisation rates c , extinction rates e , numbers of patches N , and initial numbers of occupied patches $n(0) = i$, aids species priority ranking. Additionally, if there is a wide variety of species to be compared, then either of the approximations [A1] or [A2] provides a criterion upon which to determine if more precise evaluation using [R1] (and subsequently, perhaps via simulation of a spatially-realistic model) is required. We emphasise the simplicity of our rule—the formulae may be evaluated rapidly for a host of species.

Whilst [R1] provides rapid species priority ranking, it tells us nothing about optimal strategies for those species most at risk. This is addressed by our second rule of thumb [R2].

Optimal management strategy [R2]. The management options available are to increase the colonisation rate c , say via creation or improvement of habitat corridors, or decrease the extinction rate e , say by restoring habitat or expanding patches (Etienne and Heesterbeek (2001)). The budgetary constraint can be expressed as $K_c(c^* - c) + K_e(e - e^*) \leq B$, where K_c and K_e are the respective costs for changes in c and e with B , the total budget, fixed (all evaluated over the same management period) and (c^*, e^*) is the optimal choice of c and e we seek to determine. Since any increase in c or decrease in e will always increase the expected extinction time, we will always expend our entire budget. Thus, the inequality in our budget constraint will be satisfied with equality: $\delta c = (B - K_e \delta e)/K_c$, where $\delta c = c^* - c$ and $\delta e = e - e^*$. We therefore choose the (c^*, e^*) combination that maximises the expected extinction time. From the exact formula [R1] it can be seen that we must choose ρ as small as possible, being equivalent to maximising the expected (quasi-)equilibrium number of occupied patches in the

metapopulation network. Thus, assuming there is a minimum level that the extinction rate can be reduced to, our rule of thumb is:

Invest in reducing e to its allowable minimum, unless $B < K_e e - K_c c$, in which case invest in increasing c .

Spatially-realistic models. To use our rules for spatially-realistic models, we need to calibrate our simple model (Table 1) to the more complex model (Table 2). We propose and adopt the following calibration, obtained by matching the colonisation and extinction rates (weighted by area in the spatially-realistic model, which is a good proxy for occupancy probability) when there is only a single patch occupied:

$$c := \frac{gN}{(N-1) \sum_{k=1}^N A_k} \sum_{i=1}^N A_i \sum_{\substack{j=1 \\ j \neq i}}^N \exp(-\beta \sqrt{d_{ij}}), \quad e := \frac{\kappa N}{\sum_{k=1}^N A_k}. \quad (1)$$

For testing this calibration in concert with [R1] and [R2] we randomly generated, in each case, 100 metapopulation networks and species parameters. In all cases $N = 8$, a size chosen so that the exact expected time to extinction may be evaluated (as opposed to requiring simulation to estimate the time), and because it corresponds to the size of our application species. Furthermore, for each simulation and patch $i = 1, 2, \dots, 8$, we sampled as follows: $A_i \sim U(10, 500)(\text{km}^2)$, $\text{Position}_i \sim [U(0, 20), U(0, 20)](\text{km})$, $g \sim U(0.05, 1)$, $\beta \sim U(1/5, 3/5)$, $\kappa \sim U(15, 50)$ and $n(0) \sim [\text{Ber}(1/2), \dots, \text{Ber}(1/2)]$, where $U(a, b)$ is the uniform distribution on the interval (a, b) and $\text{Ber}(p)$ is the Bernoulli distribution with success probability p .

For evaluating Rule [R1] we accepted only those generated networks for which the exact expected time to extinction was less than 500 (years) and also with the calibrated $\rho = e/c$ less than or equal to 1, corresponding to a species of (some) conservation concern, but needing to be assessed to determine the extinction risk. Additionally, we restricted attention to species with $\rho > 1/5$, noting that $\rho \leq 1/5$ typically corresponded to species near the upper limit of extinction time equalling 500 years, as our approximation method was found to consistently over estimate the expected time to extinction by a sizeable margin when $\rho \leq 1/5$; we note that this condition may be determined simply from c and e , and thus poses no impediment to use of our methodology. Finally, we also ensured that at least two patches were initially occupied. Our results are presented in Table 3, in the form of mean, median and variance of the *Relative Error* (RE) between the exact and approximated extinction time, and also the mean and median of the *Absolute value of the Relative Error* (ARE).

Statistic	Value
mean(RE)	0.0747
median(RE)	0.0512
var(RE)	0.0234
mean(ARE)	0.1159
median(ARE)	0.0748

Table 3. Spatially-realistic extinction time test results.

The statistic of most interest from Table 3 is the median absolute relative error (0.0748), which demonstrates that the approximation method typically performs well, with an over- or under-estimate of typically around 7.5%. From the median relative error, of 0.0512, we can see that typically we over estimate the extinction time.

For evaluating Rule [R2] we set $B = 1$ (without loss of generality) and then randomly generated changes, δc and δe , to the colonisation rate and local extinction rate (so both were less than the minimum of c and e); these were then used to determine the cost parameters $K_e = 1/\delta e$ and $K_c = 1/\delta c$. We then evaluated the optimal policy using [R2], and compared this to the *true* optimal policy by evaluating the exact expected extinction times with colonisation rate increased by δc and local extinction rates decreased by δe . Rule [R2] was found to give the correct policy 90% of the time. We note that out of the 100 randomly-generated metapopulation systems, the optimal policy was to increase the colonisation rate in only 13 systems, and our procedure correctly identified these cases in all instances. Thus, in 10 of the remaining 87 cases our procedure incorrectly recommended increasing the colonisation rate when in fact decreasing the local extinction rate was optimal.

Finally, we considered a species of conservation concern in Australia: malleefowl (*Leipoa ocellata*) in the Bakara region of South Australia. The species occupies an 8-patch network with patch areas and positions as detailed in

Table 4. We assume parameter values used in an earlier study (Day and Possingham (1995)): $g = 0.005$, $\beta = 1/5$ and $\kappa = 13$. We calibrated our simple model to this spatially-realistic model using (1), thus giving $c = 0.0216$ and $e = 0.0168$. The exact expected time to extinction for this malleefowl population, starting from all patches initially occupied, is 327.5 years, and our estimate using [R1] is (an impressively accurate) 323.3 years. Obviously from Figure 1 we can see that with $N = 8$ patches the approximations [A1] and [A2] should clearly not be used; for interests sake, the estimated expected time to extinction using [A1] and [A2], respectively, are 529.5 and 791.3 years. Note that the error in these estimates is close to those for similar sized patches as illustrated in Figure 1.

Patch	Area (km ²)	x-coordinate (km)	y-coordinate (km)
1	2700	6	17
2	100	14	16
3	750	18	14
4	550	11	13
5	100	19	10
6	400	6	8
7	1200	14	7
8	400	3	5

Table 4. Patch areas and positions for malleefowl habitat in the Bakara region of South Australia.

3. METHOD

For a general Markov chain with transition rates $Q = (q(m, n), m, n \in S)$, whose state space S includes a subset A which is reached with probability 1, the expected time τ_i it takes to reach A starting in state i is the minimal non-negative solution to $\sum_{j \in S} q(i, j)\tau_j + 1 = 0, i \notin A$, with $\tau_i = 0$ for $i \in A$. This result, which can be found in most texts on Markov chains, reduces the problem of computing persistence times to that of solving a system of linear equations, for which there is a host of numerical methods available. For any stochastic birth-and-death process, with sets of (population-size dependent) birth rates $\{\lambda_j\}$ and death rates $\{\mu_j\}$, τ_i is given by $\tau_0 = 0$ and

$$\tau_i = \sum_{j=1}^i \frac{1}{\mu_j \pi_j} \sum_{k=j}^N \pi_k \quad (1 \leq i \leq N), \quad (2)$$

where the ‘‘potential coefficients’’ (π_j) are given by $\pi_1 = 1$ and $\pi_j = \prod_{k=2}^j (\lambda_{k-1}/\mu_k)$ for $j \geq 2$ (see Norden (1982)), valid in the infinite state case, replacing N by ∞ . For the present static landscape model we arrive at [R1]. Whilst [R1] does not pose any significant numerical problems, a simpler (asymptotic) expression can be derived. Using [R1] we obtain the explicit asymptotic (large- N) formula [A1], which is valid when $\rho < 1$. Further approximation can be made to obtain formula [A2]. (Full details can be found in the Appendix.) The optimal management strategy rule of thumb [R2] was derived by simply choosing the option that maximised the expected number of occupied patches in quasi equilibrium. As reported above, to apply our rules to spatially-realistic models we adopted the calibration detailed in the previous section (definitions given in (1)). They were obtained by matching the colonisation and extinction rates (weighted by area in the spatially-realistic model) when there is only a single patch occupied. We emphasise that this provides an explicit procedure for approximating the spatially-realistic model by way of the simple model. Finally, the 200 metapopulation systems were generated by sampling, for each simulation and patch $i = 1, 2, \dots, 8$, as: $A_i \sim U(10, 500)(\text{km}^2)$, $\text{Position}_i \sim [U(0, 20), U(0, 20)](\text{km})$, $g \sim U(0.05, 1)$, $\beta \sim U(1/5, 3/5)$, $\kappa \sim U(15, 50)$ and $n(0) \sim [\text{Ber}(1/2), \dots, \text{Ber}(1/2)]$. We then used the exact expected time to extinction, and policy, to compare with our rules using the above mentioned calibration (1) in concert with [R1] and [R2], respectively.

4. DISCUSSION

We note that in assuming equal costs of increasing c and decreasing e , that is $K_c = K_e$ (and in fact whenever $K_c \geq K_e$), it is always optimal to invest in decreasing the extinction rate (first) if $c > e$ (Rule [R2]). This conclusion broadly supports the conclusion of Etienne and Hesterbeek (2001). Our result advances their finding by incorporating the costs of the two management strategies, meaning that for certain costs it may be optimal to invest in increasing the colonisation rate first.

We have assumed that costs are linear in the relevant variables. In reality it is likely that increasing costs will be associated with increasing changes in parameter values—small changes can be made cheaply, but further changes cost substantially more. Additionally, we have assumed that all patches are equally modified, that is, all colonisation and extinction rates are varied. With a limited budget, we may wish to target only a subset of the patches, or it might be optimal to spread the changes across patches in a weighted manner. Future research should consider these realistic modifications.

Our results provide encouragement for using rules of thumb based on simple models calibrated to more complex ones, particularly in light of previous studies reporting similar findings, for example Etienne and Heesterbeek (2001), Keeling (2002) and Ovaskainen (2002). However, the robustness of our calibration methodology and rules needs to be explored fully, for larger metapopulation systems and for other spatially-realistic models. Despite this, it appears that our methods can be used, at the very least, to greatly reduce the number of species requiring more detailed analysis, and to provide a rapid indication of the optimal management policy. We recommend that whenever feasible exact methodology be used.

5. APPENDIX

Our static landscape model is a birth-death process $(X(t), t \geq 0)$ taking values in $S = \{0, 1, \dots, N\}$ with birth and death rates $\lambda_n = (c/N)n(N - n)$ and $\mu_n = en$, where $e > 0$ and $c > 0$. Thus, S consists of an irreducible class $C = \{1, \dots, N\}$ and an absorbing state 0 which is accessible from C . It is well known that if $e > c$ the process is absorbed quickly, but, as noted earlier, if $e < c$ the population settles down to a quasi equilibrium that may persist for a long period. In this latter case, the carrying capacity is $(1 - \rho)N$, where $\rho = e/c$. We are interested in the expected time $\tau_i(N)$ it takes for the process to reach 0 starting in state i for a given ceiling N . For a general birth-death processes on S with birth rates $\{\lambda_n\}$ and death rates $\{\mu_n\}$, $\tau_i = \tau_i(N)$, for $i \geq 1$, is given by (2). For our model, it is given by [R1]. Several authors have derived asymptotic expansions like our [A1]. Kryscio and Lefèvre's (1989) formula (2.4) (for the case $\rho < 1$) is at variance with our formula [A1].

In what follows, $a_N \sim b_N$ means $a_N/b_N \rightarrow 1$ as $N \rightarrow \infty$.

Theorem 1. If $\rho < 1$, then as $N \rightarrow \infty$,

$$\tau_i(N) \sim \frac{1}{c(1 - \rho)} \left\{ \left(\frac{1 - \rho^i}{1 - \rho} \right) \left(\frac{e^{-(1 - \rho)}}{\rho} \right)^N \sqrt{\frac{2\pi}{N}} - \sum_{k=1}^{i-1} \frac{(1 - \rho^{i-k})}{k} \right\}.$$

Proof. The plan is to evaluate the factorials implicit in [R1] as gamma integrals and then invoke standard asymptotic results. We use Laplace's method (see Section 12.2.5 of Olver (1983)) to estimate the integrals. Let σ_j be the expected first-passage time to state $j - 1$ from state j , so that $\tau_i(N) = \sum_{j=1}^i \sigma_j$. Then,

$$\sigma_j = \frac{1}{\mu_j \pi_j} \sum_{k=j}^N \pi_k = \frac{w^j (N - j)!}{eN!} \sum_{k=j}^N \binom{N}{k} \frac{(k - 1)!}{w^k},$$

where $w = \rho N$, this being true for $j = 1, \dots, N$. Now, evaluating the factorial as a gamma integral gives

$$\sigma_j = \frac{w^j (N - j)!}{eN!} \sum_{k=j}^N \binom{N}{k} \int_0^\infty e^{-wx} x^{k-1} dx = \frac{\rho^j}{e} \frac{N^j}{N(N - 1) \cdots (N - j + 1)} \int_0^\infty \frac{e^{-\rho Nx}}{x} \sum_{k=j}^N \binom{N}{k} x^k dx. \quad (3)$$

Since $\sum_{k=j}^N \binom{N}{k} x^k = (1 + x)^N - \sum_{k=0}^{j-1} \binom{N}{k} x^k$, the above integral becomes (after substituting $s = N\rho x$)

$$\int_0^\infty \frac{e^{-s}}{s} \left\{ \left(1 + \frac{s}{N\rho} \right)^N - \sum_{k=0}^{j-1} \binom{N}{k} \left(\frac{s}{N\rho} \right)^k \right\} ds.$$

We now use Laplace's method to estimate the integral in (3), which can be written

$$\int_0^\infty \frac{e^{-\rho Nx}}{x} \left\{ (1 + x)^N - \sum_{k=0}^{j-1} \binom{N}{k} x^k \right\} dx = \int_0^\infty e^{Nr_N(x)} q(x) dx,$$

where $q(x) = 1/x$ and $r_N(x) = -\rho x + (1/N) \log \left((1 + x)^N - \sum_{k=0}^{j-1} \binom{N}{k} x^k \right)$. For all $x > 0$ and $j \geq 1$, $\lim_{N \rightarrow \infty} \left((1 + x)^N - \sum_{k=0}^{j-1} \binom{N}{k} x^k \right)^{1/N} = 1 + x$, and so $r_N(x) \rightarrow r(x)$, where $r(x) = -\rho x + \log(1 + x)$.

However, we get no useful information if we base our approximation on an estimate of $\int_0^\infty \exp(Nr(x))q(x) dx$, because this integral is divergent for any N . Instead, we estimate $\int_0^\infty (e^{-\rho Nx}/x) \{(1+x)^N - 1\} dx = \int_0^\infty e^{Ns_N(x)}q(x) dx$, where $s_N(x) = -\rho x + (1/N) \log((1+x)^N - 1)$. First, since $r'(x) = 1/(1+x) - \rho$ and $r''(x) = -1/(1+x)^2$, it is clear that r achieves its maximum at $a = 1/\rho - 1$. We deduce that $s_N(x)$ achieves its maximum near $a = 1/\rho - 1$. So, employing Laplace's method, we get in the limit as $N \rightarrow \infty$,

$$\int_0^\infty e^{Ns_N(x)}q(x) dx \sim q(a)e^{Nr(a)}\sqrt{\frac{2\pi}{-Nr''(a)}} = \frac{1}{1-\rho} \left(\frac{e^{-(1-\rho)}}{\rho}\right)^N \sqrt{\frac{2\pi}{N}}.$$

Therefore,

$$\sigma_j \sim \frac{\rho^j}{c(1-\rho)} \left(\frac{e^{-(1-\rho)}}{\rho}\right)^N \sqrt{\frac{2\pi}{N}} - \frac{\rho^j}{e} \sum_{k=1}^{j-1} \frac{\rho^{-k}}{k}.$$

Summing over j from 1 to i , and using an earlier calculation, gives the stated result.

Approximation [A2] is then achieved using $\sum_{k=1}^{i-1} (1 - \rho^{i-k})/(k(1 - \rho)) \approx \gamma + \ln(i - 1)$, by taking the ratio $(1 - \rho^{i-k})/(1 - \rho) \approx 1$ (noting that this ratio is in fact less than or equal to 1) and taking a first-order approximation to the digamma function in the resulting $(i - 1)$ th harmonic number.

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