A Revised Assessment of Species Redundancy and Ecosystem Reliability

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Introduction

Naeem (Conservation Biology 12:39–45) formalized the relationships among species diversity, functional groups, species redundancy, and ecosystem reliability. Although we applaud his efforts and agree with many of his conclusions, we disagree with some fundamental assumptions used in the derivation of Naeem’s equation 2. These assumptions affect some of the conclusions concerning the role of redundancy. We discuss two possible interpretations of Naeem’s equation. Under the first interpretation, the equation relates to the probability that a species is present at a particular time \( t \). Under the second interpretation, the equation relates to the probability that a species is present at least once during the interval of time between time 0 and time \( t \). Under this second interpretation we also disagree with the application of Naeem’s equation 4.

In his equation 2, Naeem relates “the probability that the \( i \)th species in the \( j \)th functional group is present by time \( t \)” to the probability that the initial population survives until time \( t \) and the probability of colonization by time \( t \), as follows:

\[
R_{ij}(t) = P_{ij}(t) + C_{ij}(t) - P_{ij}(t)C_{ij}(t),
\]

where \( R_{ij}(t) \) is the probability that the species is present by time \( t \), \( P_{ij}(t) \) is the probability that the initial population survives until time \( t \), and \( C_{ij}(t) \) is the probability that the site has been colonized by the species by time \( t \). He argues correctly that \( R_{ij}(t) = e^{-\lambda_{ij}t} \) and \( C_{ij}(t) = 1 - e^{-\nu_{ij}t} \), where

\[
\lambda_{ij} = \lim_{\Delta t \to 0} \frac{p_{ij}}{\Delta t}, \quad \nu_{ij} = \lim_{\Delta t \to 0} \frac{q_{ij}}{\Delta t},
\]

and \( p_{ij} \) and \( q_{ij} \) are, respectively, the probabilities of extinction and colonization during time interval \( \Delta t \). With this formulation, \( R_{ij}(t) \) drops initially from 1 and then, after a transient dip, increases asymptotically back toward 1 as \( C_{ij}(t) \) comes to dominate the dynamics (Fig. 1).

Interpretation 1

Under the first interpretation of the Naeem equations, we question this asymptotic approach toward 1 because it implies that every species should be present after a sufficiently large \( t \). We believe that a more appropriate model is one in which the colonizing population can subsequently face extinction. We therefore provide the following derivation as a more realistic representation of \( R_{ij}(t) \).

We base the derivation on the potential occurrences during an infinitesimal time interval \( dt \). Three probabilities need to be considered over this time interval: (1) the probability that the species is present at the beginning of the interval \( (R_{ij}(t)) \); (2) the probability that the species goes extinct during the time interval \( (\lambda_{ij} dt) \); and (3) the

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probability that the species colonizes during the time interval ($\nu_{ij} \Delta t$). We assume that the time period is short enough that the probabilities of multiple extinction-colonization events during the time interval can be neglected.

As in Naeem’s derivation, we assume that $\lambda_{ij}$ and $\nu_{ij}$ are constant. This assumption implies that changes in the competitive interactions with other species, in the proximity of sources of propagules, in resource availability, and in the genetic characteristics of the population can be ignored.

Because the possibility of local extinction is contingent upon the species being initially present, and because the possibility of colonization is contingent on the species either not being initially present or going extinct within the time interval, five possible combinations of events can occur during the time interval. The probabilities for these events can be calculated as follows:

1. initially present, becomes extinct, colonizes, $R_{ij}(t) \lambda_{ij} \nu_{ij}$
2. initially present, becomes extinct, does not colonize, $R_{ij}(t) \lambda_{ij}(1 - \nu_{ij})$
3. initially present, does not become extinct, $R_{ij}(t)(1 - \lambda_{ij})$
4. not initially present, colonizes, $(1 - R_{ij}(t)) \nu_{ij}$; and
5. not initially present, does not colonize, $(1 - R_{ij}(t))(1 - \nu_{ij})$

It is easily demonstrated that these five events encompass all the relevant occurrences because their probabilities sum to 1 (i.e., one of the five events must occur during the time interval).

Of these five events, events one, three, and four result in the species being present at time $t + \Delta t$. The probability that the species is present at time $t + \Delta t$ is the sum of the probabilities associated with these events:

$$R_{ij}(t + \Delta t) = R_{ij}(t)\lambda_{ij} \nu_{ij} + R_{ij}(t)(1 - \lambda_{ij}) + (1 - R_{ij}(t))\nu_{ij}.$$  

(2)

From this equation the rate of change of the probability of the species being present at time $t$ can be calculated as

$$\frac{dR_{ij}(t)}{dt} = R_{ij}(t + \Delta t) - R_{ij}(t)$$

$$= R_{ij}(t)(\lambda_{ij} \nu_{ij} - \lambda_{ij} - \nu_{ij}) + \nu_{ij}.$$  

(3)

Integrating and imposing the condition that the species is present at time 0 yields the following relationship, which we propose as a replacement for Naeem’s equation 2:

$$R_{ij}(t) = \frac{\nu_{ij} - \lambda_{ij}}{\lambda_{ij} \nu_{ij} - \lambda_{ij} - \nu_{ij}} e^{(\lambda_{ij} \nu_{ij} - \lambda_{ij} - \nu_{ij})t} - \nu_{ij}.$$  

(4)

This equation yields the conditional probability that the species will be present at time $t$ if it was present at time 0. The conditional probability that the species is present at time $t$ if it was absent at time 0 can also be calculated by replacing the $(\lambda_{ij} \nu_{ij} - \lambda_{ij})$ coefficient of the exponential term in the numerator with $\nu_{ij}$.

Our equation does not result in a transient dip followed by an unrealistic approach toward an asymptote of 1 (Fig. 2). Rather, our equation monotonically approaches an asymptote of $\nu_{ij}/(\lambda_{ij} + \nu_{ij} - \lambda_{ij} \nu_{ij})$. That is, the long-term probability that the species will be present at time $t$ will increase as the probability of colonization increases and will decrease as the probability of local extinction increases. This long-term probability is independent of whether the species is present or absent at time 0.

With this equation for $R_{ij}$, Naeem’s equations 3 and 4 can be used to calculate the probabilities of services being provided by ecosystems at time $t$ (“ecosystem reliability”) as the number of functional groups ($M$) changes and as the number of species within functional groups ($S$, species redundancy) changes (Fig. 5). This analysis indicates that the ecosystem reliability is also monotonically asymptotic. Importantly, Naeem’s conclusion that “increasingly more complex ecosystems (higher values of $M$) are less reliable . . . , but increasing species redundancy (higher values of $S$) can compensate for reduction in reliability” need not be qualified with the phrase “over short periods of time.” Under the first interpretation of the Naeem equations, the reliability of an ecosystem providing a function at some future time $t$ can never be 100% as long as the probability of local extinction for all the species within a functional group is greater than zero.

**Interpretation 2**

Under the second interpretation, Naeem’s equation 2 applies to the probability of a species being present at least

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**Figure 2.** A revised representation of the probability that a species is present in an ecosystem ($R(t)$) at time $t$ as a function of the instantaneous probabilities of local extinction ($\lambda$) and colonization ($\nu$) over time.
once in the time interval between time 0 and time t. In this interpretation, we question the transient decrease in the probability of a species being present (Fig.1) because it implies that the probability that the species is present during a short interval of time is greater than the probability that the species is present in a longer interval of time that includes the shorter interval. If the species is present in the shorter interval, it must be present in the longer interval and thus the probability cannot decrease.

The cause of this transient decrease in probability is the inclusion of the potential extinction of an initially present population in the derivation of Naeem’s equation 2. We believe that a more appropriate model is one based on the probability that an initial population even exists and ignores any subsequent extinction of that population or of any colonizing population. Once the species is present, any subsequent extinction is irrelevant. This model is easily incorporated into Naeem’s equation 2 (our equation 1) by replacing \( P_y(t) \) with the probability that there is an initial population. In the absence of any prior knowledge of when the species might have been present in the past, the best estimate of this probability is the asymptote of the function we derived above (our equation 4). That is, \( P_y(t) \) in Naeem’s equation 2 (our equation 1) should be replaced with a constant equal to \( \frac{v_y}{\lambda_y + v_y - \lambda_y v_y} \).

With this substitution, the probability that the species is present at least once in the time period from time 0 to time \( t \) increases monotonically from \( \frac{v_y}{\lambda_y + v_y - \lambda_y v_y} \) toward an asymptote of 1 as \( t \) increases. Naeem’s equation 3 can then be used to calculate the probability that a functional group of species provides its service. But Naeem’s equation 4 can only be used to calculate the probability of the ecosystem providing a service if the functional groups interacting to provide that service need not act sequentially. To accommodate a sequential interaction, the equation has to be modified to reflect the probability that the functional groups that act later in the sequence are present after the functional groups that act earlier in the sequence. For example, Naeem’s equation 4 in its present form allows the ecosystem service to be performed even if a functional group acting late in the sequence were present initially but went extinct and a functional group acting early in the sequence were absent until after this extinction.

It is difficult to write a general expression for the probability of ecosystem services that require sequential interactions among functional groups. For the case of three functional groups, the equation is as follows (functional groups are numbered in order of their appearance in the sequence):

\[
H(t) = F_1(0)F_2(0)F_3(0) + F_1(0)F_2(0)
\int_0^t G_3(\tau_3) d\tau_3 + F_1(0)F_3(0)\int_0^t G_2(\tau_2) d\tau_2 + F_2(0)F_3(0)\int_0^t G_1(\tau_1) d\tau_1 +
\int_0^t \int_0^{t-\tau_1} G_1(\tau_1)G_3(\tau_3) d\tau_3 d\tau_1 + F_3(0)
\int_0^t \int_0^{t-\tau_1} G_1(\tau_1)G_2(\tau_2) d\tau_2 d\tau_1 +
\int_0^t \int_0^{t-\tau_1} \int_0^{\tau_1} G_1(\tau_1)G_2(\tau_2)G_3(\tau_3) d\tau_3 d\tau_2 d\tau_1,
\]

where \( F_j(t) \) is calculated from Naeem’s equation 3 with our modification of his equation 2; \( F_j(0) \) is the probability
of the functional group being present during any infinitesimally short time interval given no information of prior presence or absence (i.e., the probability of it being present at any particular time), \( G_j(t) = (1 - F_j(t))Y_j \); and

\[
Y_j = \sum_{i=1}^{s_j} a_{ij}
\]

is the instantaneous colonization rate for functional group \( j \) (i.e., \( Y_j dt \) is the probability that at least one of the species in functional group \( j \) colonizes during the interval \( dt \)). The first term in the equation is the probability that all functional groups are initially present. The second term is the probability that functional groups one and two are initially present and that functional group three is initially absent but colonizes some time prior to time \( t \). The third term is the probability that functional group one is initially present, that functional group two is initially absent but colonizes at sometime prior to time \( t \), and that functional group three is present at the time that functional group two colonizes. The fourth term is the probability that functional group one is initially absent but colonizes sometime prior to time \( t \) and functional groups two and three are present at the time of that colonization. The fifth term is the probability that functional group one is initially present, that functional group two is initially absent but colonizes prior to time \( t \), and that functional group three is absent at the time functional group two colonizes but colonizes sometime thereafter but before time \( t \). The sixth term is the probability that functional group one is initially absent but colonizes sometime prior to time \( t \), that functional group two is present and functional group three absent at the time of that colonization, and that functional group three colonizes sometime thereafter but prior to time \( t \). The seventh term is the probability that functional group one is initially absent but colonizes sometime before time \( t \), that functional group two is absent at the time of that colonization but colonizes sometime thereafter but before time \( t \), and that functional group three is present at the time functional group two colonizes. The final term is the probability that functional group one is initially absent and that the three functional groups then colonize sequentially but are absent at the time that the prior functional group in the sequence colonizes.

Our equation 5 can be related to Naeem’s equation 4 by noting that

\[
F_j(t) = F_j(0) + \int_0^t G_j(\tau_j) dt \tau_j.
\]

With this expression for \( F_j(t) \), our equation 5 is identical to Naeem’s equation 4 written in expanded form, except that the limits on some of the integrals have been truncated to account for the sequential nature of the interactions among functional groups. Specifically, in any term containing more than one integral, the integral relating to any higher-numbered functional group \( j \) has been incorporated within the integrals of the lower-numbered functional groups \( (j) \) and the upper limit on the higher-numbered integral has been decreased from \( t \) to

\[
t - \sum_{j<i} \tau_j,
\]

where the summation is over all lower-numbered \( \tau_j \) in the same term. With this rule, our equation 5 can be extended to any number of functional groups.

Our equation 5, applied to \( n \) functional groups, results in a monotonic increase from an initial value of

\[
\prod_{j=1}^{n} F_j(0)
\]

to an asymptote of 1, as will Naeem’s equation 4 with our suggested modification of his equation 2. Because of the modifications to account for sequential interactions, however, our equation approaches this asymptote more slowly. This lag behind the Naeem equation is more pronounced for high extinction rates and low colonization rates.

We suggest one additional improvement to our equation 5. The services provided by the individual functional groups should have a maximum useful duration before they need to be renewed. For example, if the decomposers release available nitrogen in year one, that nitrogen will be of little use if the primary producers are absent until year 10. If this maximum useful duration is less than the upper limit on the integrals associated with the functional group making use of that service (i.e., the next functional group in the sequence), then that limit should be replaced by that maximum useful duration. Under the second interpretation of the Naeem equations, the inclusion of a maximum useful duration on the services provided by even one functional group will result in the long-term ecosystem reliability being less than 100% as long as the species in that functional group can go extinct.

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