Co-evolved Species and Intertwined Risks of Extirpation

Species whose co-evolution has made them reciprocal factors in defining their habitats are major components of our approach to habitat analysis. In addition to identifying general biotic factors of importance, we list known symbiotic or competitive associations between species that represent important adaptations to their environment and that, consequently, play major roles in selecting where they choose to live.

As components of biodiversity, these ecological relationships are conservation targets in their own right and deserve as much attention as has traditionally been given to survival needs of individual species. Pitcher Plants (*Sarracenia* species), for instance, are amazing species in terms of their individual adaptations to their environment, especially the evolution of the mechanisms involved in capturing insect prey to supplement what they get from their nutrient-poor habitats. Just as amazing, however, are the large number of symbionts they support. These species are equally impressive in their adaptations to avoid being captured and consumed by their host plants and in their specialized uses of the pitchers as a food source, shelter, or specialized aquatic habitat. These symbionts include obligate herbivores as well as commensals and mutualists with respect to their interaction with the Pitcher Plants themselves. These species further interact with each other in their own competitive, predatory, and mutualistic relationships. In their entire sets of interactions, these groups of organisms represent microcosms of ecosystems more generally.

In the conservation of Biodiversity – involving the protection of both individual taxa and their ecological inter-relationships – highly complicated, long-evolved associations clearly deserve to be given as much attention as the individual species that are involved. In this paper, we describe these interactions within a probabilistic framework and select methods of analysis that make use of this information in setting conservation priorities.

Rather than focus on the variety and complexity of the co-evolved relationships directly, we concentrate our attention on the tight intertwining of the fates of the involved species that results from those interactions. Loss of any one of these species has implications, both positive and negative, for the survival of the others, and it is those consequences that we make use of in determining the priority for conservation of these entire sets of interacting species. For example, loss of Purple Pitcher plants – either across their entire range or just individual populations – will lead to the extirpation of their obligate symbionts, including their herbivores, commensals, and mutualists. Loss of those symbionts, conversely, may lead to either increased survival of their host plants or decreased viability, depending on the relationship. Analysis of these reciprocal effects on the probabilities of extirpation of the entire group is the goal of our approach.

Although it would be most realistic to recognize the dynamic nature of imperilment, changing constantly over time, we rarely have real-time data coming in that would allow timely re-adjustments to our probability estimates; whenever such updates are available, we do, in fact,

adjust our estimates. More generally, however, we take a discrete approach to the analysis of these intersecting probabilities of extirpation: we estimate these probabilities for a set period of time and consider them to be static during that period. This is similar to the approach used by NatureServe and the Natural Heritage Program network in setting global and state ranks that estimate the probabilities of survival in terms of ten-year periods.

In fact, we rely extensively on the State Ranks established by NHP as the basis for estimating probabilities of extirpation. We follow their assigning risk status for individual species according to five discrete categories and also use of ranges of these values to indicate uncertainties in these estimations. Our approach differs, however, in that we interpret these risk categories in terms of probabilities of extirpation rather than the indirect, ordinal level estimates used by NHP. The model we developed for this purpose is described in a separate document (see *Use of NHP/NS State Ranks to Estimate Species' Risks of Extirpation*, found under Habitat Conservation on the home page of this website).

While the ordinal-level ranks work quite well when used to sort individual species into categories based on their level of concern, they are less useful when it comes to assessing the risks of extirpation for entire groups of species. At best, conversion of ordinal values into arbitrary numeric values can be used only as a rough index of group imperilment. Use of extirpation probabilities, on the other hand, allows analysis of group effects based on the mathematics of probability theory. While we would prefer that probabilities of extirpation be estimated directly rather than modeled, we hope at the very least that the analysis we employ in this website will spur more interest in the development of more direct estimates for species' separate probabilities of extirpation (see *A Probabilistic Approach to Estimating State Ranks*, found under Habitat Conservation on the home page of this website), as well as stimulate greater interest in considering the reciprocal relationships between species that strongly influence the survival or extirpation of entire groups.

A General Model of Reciprocal Conditional Probabilities of Extirpation

Given Probabilities of Extirpation (PEs) for individual species, the relationship between extirpation events within a group of species can be investigated using the techniques of probability theory. In particular, we are interested in the reciprocal relationships between species: how the extirpation of one species affects those of any species with which it is closely associated and conversely, how the extirpation of the associated species affects the subject species.

We start by examining cases involving just two species, whose interactions must be considered in any group of species and whose properties can be extrapolated in considering the inter-relationships among more than two species. The Venn diagram below shows the combination of the three possible extirpation events involving the species labeled S1 and S2.
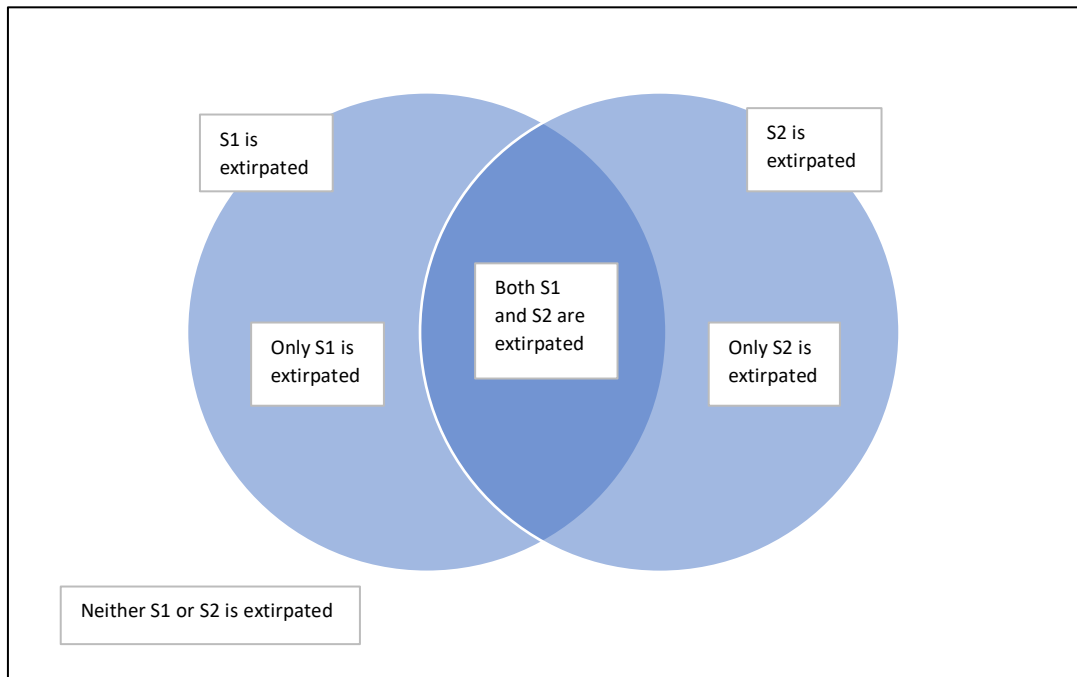
The event where S1 is extirpated is represented by the circle on the left and has a total probability of occurring equal to P(S1e); in our case, this information is generally based on direct observation of the species' status in the state. Likewise, the circle on the right indicates the extirpation of S2, with the probability occurrence equal to P(S2e).

The three sectors created by the intersection of these two circles each represent a different extirpation event. The crescent on the left corresponds to the extirpation solely of S1; the one on the right, the extirpation of solely S2; and the lens in the center representing the even where both species become extirpated. The event where neither species becomes extirpated is also shown, represented by the space surrounding the intersecting circles.

Where three of these probabilities are known -- including at least one of the overall probabilities for the species -- the probabilities of each of the three events can be easily calculated using the axioms of probability theory. In the cases described below, we assume that both of the PE values are known for the species. In our analysis of reciprocal relationships, we also need to know both of the conditional probabilities of the extirpation of one species given knowledge of extirpation of the other. In other words, we need to know all of the following:

P(S1e)
P(S2e)
P(S1e|S2e)
P(S2e|S1e)

where the pipe symbol represents "given that"; e.g., P(S1e|S2e) refers to the probability that S1 becomes extirpated given knowledge that S2 has become extirpated.

Depending on which species becomes extirpated first, different probabilities for the three extirpation events shown in the above figure can differ greatly. In the following example, representing a case of commensalism, the extirpation of S1, the host species, is independent of the extirpation of S2, the commensal:

P(S1e|S2e) = P(S1e)

In other words, the information that commensal has been extirpated has no effect on the probability of extirpation of host species.

For the commensal, on the other hand, the extirpation of the host species has major consequences for its own survival:

P(S2e|S1e) > P(S2e).

For obligate commensals, the conditional probability is equal to 1.0, whatever the value is for P(S2e) overall. The example below is based on the following specified values:

P(S1e) = 0.8
P(S2e) = 0.9
P(S1e|S2e) = 0.8
P(S2e|S1e) = 1.0

Assuming first that it is the commensal (S2) that has been extirpated, we can calculate the three extirpation events as follows. For the event where both species become extirpated (note that the ∩ symbol means "and"):

P(S1e ∩ S2e) = P(S2e) x P(S1e|S2e) = P(S2e) x P(S1e) = 0.8 x 0.9 = 0.72

For the event where S1 becomes extirpated by itself, we can use the following calculation, based on the figure given above (note that the apostrophe is used to indicate the complement of the probability, i.e., the survival of species):

P(S1e ∩ S2e') = P(S1e) – 0.72 = 0.08

This follows in that the overall probability of S1 becoming extirpated is equal to the probability of its becoming extirpated by itself plus the probability that it becomes extirpated at the same time as S2.

Similarly, the probability of S2 becoming extirpated by itself is:

P(S2e ∩ S1e') = P(S2e) – 0.72 = 0.9 – 0.72 = 0.18.

Ignoring the total number of extirpations associated with these events, each of the three events represents a mutually exclusive event where at least one extirpation (ALOE) has taken place. The sum of these probabilities, thus, estimates the probability that any extirpation will take place, given knowledge that S2 has become extirpated:

P(ALOE)|S2e = 0.72 + 0.08 + 0.18 = 0.98

When the situation is reversed, and it is knowledge that host species (S1) that has become extirpated, we get a very different set of probabilities:

P(S2e ∩ S1e) = P(S1e) x P(S2e|S1e) = 1.0 x 0.8 = 0.8
P(S2e ∩ S1e') = P(S2e) – 0.8 = 0.9 – 0.8 = 0.1
P(S1e ∩ S2e') = P(S1e) – 0.8 = 0

Summing these values:

P(ALOE)|S1e = 0.9

If we consider the condition that S1 becomes extinct first is mutually exclusive to the event S2 becomes extinct first, then we can calculate the combined value of P(ALOE), given that one or the other of the two species has become extirpated, by averaging the values (making use of the probabilities that each species will become extirpated) :

{[P(S2e) x 0.98] + [P(S1e) x 0.9]} / [P(S1e) + P(S2e)] =
[(0.9 x 0.98) + (0.8 x 0.9)] / (0.8 +0.9) = 0.94

This example illustrates both the need to specify both the two conditional probabilities of extirpation in addition to the overall probabilities of extirpation of the two species, and that the outcome – the probability of any extirpation taking place within this pair of species – must take into account the knowledge of each species becoming the first to be extirpated. The following section uses this information on the reciprocal effects of extirpation to categorize the various forms of species interactions.

Probabilistic Characterization of Two-Species Relationships

Symbiotic and antagonistic relationships between pairs of species have traditionally been defined based on the harm or benefit each species gains from their interaction. In the case of host- commensal interactions, the host receives neither benefit nor harm from the relationship but the commensal directly benefits from it, and in some cases cannot survive at all without the presence of the host. As shown in the above example, "harm" can be interpreted as an increase in the probability of extirpation, given the extirpation of the other species, and "benefit" can be considered as a decrease in the probability of extirpation (note that "survival"

– a more positive term – is simply the compliment of "extirpation", i.e., P(Se') = 1-P(Se); they convey exactly the same information).

Where the two conditional probabilities are known in addition to the overall probabilities of the species' extirpations, then the traditional classification of two-species relationships can be categorized as follows:

Relationship	Probabilities for S1|S2e	Probabilities for S2|S1e
Independent Species	P(S1e|S2e) = P(S1e)	P(S2e|S1e) = P(S2e)
Host (S1) – Commensal (S2)	P(S1e|S2e) = P(S1e)	P(S2e|S1e) > P(S2e)
Amensal Agent (S1) – Amensal Casualty (S2)	P(S1e|S2e) = P(S1e)	P(S2e|S1e) < P(S2e)
Host (S1) – Phage (S2)	P(S1e|S2e) < P(S1e)	P(S2e|S1e) > P(S2e)
Mutualist (S1) – Mutualist (S2)	P(S1e|S2e) > P(S1e)	P(S2e|S1e) > P(S2e)
Antagonist (S1) – Antagonist (S2)	P(S1e|S2e) < P(S1e)	P(S2e|S1e) < P(S2e)

An understanding of these two-species cases can be important in its own right. From the example given above, it is clear that the extirpation probabilities of the two species are tightly intertwined. Even in the case where the two species are independent, that independence itself needs to be demonstrated by the observation of the conditional probabilities for the two species. Instead, independence is often just assumed, mainly to allow estimation of the overall extirpation probability of a given species based solely on its abundance, distribution, and observed population trends.

That approach is acceptable if the contribution to the extirpation of the individual species is believed to take relationships with other species into account. That, however, assumes that observations have been made both where the other species survive and where they have been extirpated (i.e., where the effects of the conditional probabilities are included, at least indirectly).

Where the conditional probabilities have themselves been directly observed, then one or the other of the two PE values can be checked by calculating it using the information provided by the PE for the other species and the observed conditional probabilities for both species. Identifying one species, SC, that has the more certain conditional probabilities, and the other, SU, that has the less certain values, we can then determine the PE for SU as follows.

P(SUe) = [P(SCe) x P(SUe|SCe)] + [P(SCe') x P(SUe|SCe')]

If this value is close to the estimate originally obtained for that species, then we can accept the null hypothesis that all of the values are acceptable. If on the other hand, the calculated value is quite different (statistical tests are needed to define that conclusion), we reject the null hypothesis with the conclusion that all of the values – PEs as well as the conditional values – need to be re-examined.

The two-species interactions, as categorized above, also play key roles in multi-species aggregations: where multiple species are involved, the conditional probabilities all represent mixtures of these two species interactions, with positive, negative, or neutral effects. As in the two-species cases, knowledge of both the individual species probabilities of extirpation (PEs) and the various conditional probabilities allows calculation of the Probability of At Least One Extirpation taking place. Given the potential complexity of these interactions as well as the difficulty in observing the conditional probabilities, use of P(ALOE) to estimate risk of extirpation for entire groups is extremely limited. It has been used for that purpose only in the limited case where all species involved in a complex are believed to be independent in their extirpation probabilities (e.g., see Smith and Zollner, 2005). In the analysis of the co-evolved complexes we are particularly interested in, such assumptions are clearly not met. Fortunately, there is another method involving the calculation of the Expected Number of Extirpations within a given place and time period that does not have these limitations and has a number of other advantages in addition (see review by Nicholson and Possingham, 2006).

Use of the Expected Number of Extirpations as a General Measure of Group Risk

In probability theory, the Expected Value of a given variable is calculated by summing the values of that variable multiplied by their probabilities of occurrence, i.e., they represent the mean value of that variable. With respect to probabilities of extirpation, this method involves the simple addition of the PEs for each species, whether or not there are any interdependencies between them. The resulting values of ENE represents a ratio-level measurement, allowing addition, multiplication, or division to produce other meaningful values.

As a measure of the extinction risk for a group of species, ENE seems almost too good to be true. However, its properties can be demonstrated fairly easily. Using the same two-species case described above, the probabilities calculated for each of the three extirpation events – each representing a mutually exclusive combination of extirpations – can be multiplied by the number of extirpations they represent. In the case where S2 is extirpated first, the following values are obtained (note that the second two probabilities include only one extirpation, along with one survival):

P(S1e ∩ S2e) x 2 extirpations = 0.72 x 2 = 1.44
P(S1e ∩ S2e') x 1 extirpation = 0.08
P(S2e ∩ S1e') x 1 extirpation= 0.18.

Summing these values produces and ENE of 1.7.

In the case where S1 is extirpated first:
P(S2e ∩ S1e) x 2 extirpations = 0.8 x 2 = 1.6
P(S2e ∩ S1e') x 1 extirpation = 0.1

P(S1e ∩ S2e') x 1 extirpation = 0

Again, a value of 1.7 is produced for the ENE despite the fact that the probabilities of the individual events are quite different for the two conditions. Averaging the two results also gives the same answer of 1.7 expected extirpations for this pair of species.

The following Venn diagram for three species provides a visual explanation for these results.
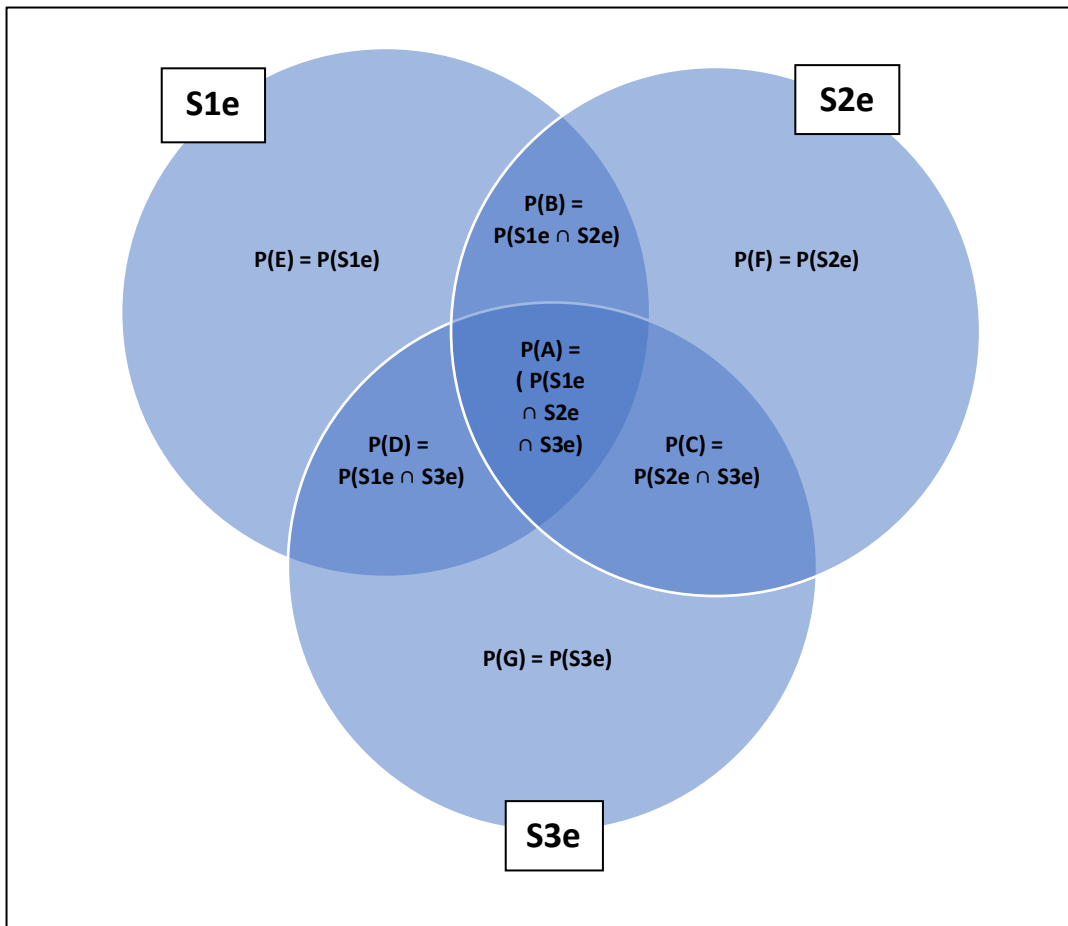
In this example, there are now seven different extirpation events, each representing a different combination of species. As in the two-species case, the three total extirpation probabilities are known for the species, as well as the conditional probabilities involved in each of the seven events. Again, the probabilities for these events are expected to differ, given which of the three species becomes extirpated first.

Rather than go to the trouble of working out all of these calculations, as we did for the much simpler two-species case, we simply assume that the probabilities have been solved for each of

the events, which are labeled A through E in the diagram. Given that Event A represents three extirpations; B, C, and D each representing two extirpations; and E, F, and G representing single extirpations, we get the following:

ENE = [3 x P(A)] + [2 x P(B)] + [2 x P(C)] + [2 x P(D)] + [1 x P(E)] + [1x P(F)] + [1 x P(G)]

Expanding these terms, we get:

ENE = P(A) + P(A) + P(A) + P(B) + P(B) + P(C) + P(C) + P(D) + P(D) + P(E) + P(F) + P(G).

Note that all of these sectors are divided along the lines representing the intersection of the events represented by each species becoming extirpated. All of the sectors enclosed within the circle for a given species represent the separate extirpation probabilities in which it takes part and the sum of all of these probabilities must equal the total PE value for the species. For example:

P(S1e) = P(E) + P(A) + P(B) + P(D)

Re-arranging the terms of the expanded version of ENE given above, we get:

ENE = [P(E) + P(A) + P(B) + P(D)] + [P(F) + P(B) + P(C) + P(A)] + [P(G) + P(C) + P(D) + P(A)],

which simplifies to:

ENE = P(S1e) + P(S2e) + P(S3e).

Calculation of ENE in this example, thus requires only the information on the overall probabilities of extirpation of the species, no what the probabilities are for each of the seven extirpation events. It does not matter whether the probabilities of extirpation of the three species are independent or dependent on one another. It also does not matter which of the three species is extirpated first – potentially producing very different probabilities for each of the seven events. As in the two-species case, the average value measured over all possible combinations will simply equal the sum of the PE values for the three species.

By extension, this method can be applied to any set of species, no matter how many there are or what interdependencies exist between their extirpation events. In all cases, the intersection of the species' probabilities produces a partition of extirpation events, dividing along the lines representing each species' combined probability of extirpation; within any species' circle, the probabilities of all separate events must equal the total PE for that species. Summing the values of each event multiplied by the number of extirpations that are included within that event will always be equivalent to simply adding the individual species' PE values together.

This is true whether or not the extirpation probabilities of the species are independent of one another or highly inter-dependent. This does not mean, however, that ENE is not affected by

any interdependencies that do occur between species. Instead, it assumes that these relationships are all accounted for in the total probabilities of extirpation for each of the included species. ENE, in this sense, simply summarizes all of these complex interactions.

This universal applicability, furthermore, is not the only desirable feature of ENE. As mentioned previously, ENE is a ratio-level variable. It has a true value of zero, which occurs where all species within a group are completely secure, i.e., having no probabilities of extirpation. The intervals between unit values, e.g., 1, 2, 3, … are also uniform, with a group that has an ENE of two having twice as many predicted extirpations as one that has an ENE of one and an ENE of three having three times as many. These properties allow the ENE calculated for that group to be directly compared to that of other groups to determine which are the more imperiled and by how much. For example, a group of species that has a value of ENE of 10 can be considered twice as imperiled as one that has an ENE value of 5, i.e., twice as many species are predicted to be lost for the first group in a specified period of time and place as for the second group. All other things being equal, the first group merits a much higher degree of conservation concern, meaning a higher level of effort and monetary expenditure should be devoted to its preservation.

Similarly, where two groups have the same number of species but where the ENE value of one is much higher due to its inclusion of species with a higher average value of PE, the group with the higher ENE merits the greater degree of concern. In addition to ENE by itself, we also make extensive use of the average PE value for groups of species, which is simply ENE divided by the number of species in the group. In particular, we can compare this value with the probabilities of extirpation estimated for single species based on the state ranks assigned by the Natural Heritage/NatureServe Network. An average PE of 0.0460 is equivalent under our model (see Use of NHP State Ranks to Estimate Species' Risks of Extirpation) of an NHP State Rank of S2, which is interpreted as having a high degree of conservation significance. Based on this interpretation, a group of 10 species that have an average PE equivalent to an S2 clearly has more conservation significance than a group of 5 species having that same average value. Just as clear, a group of 10 species with an average PE equivalent to a state rank of S1 should be given a much higher conservation significance than a group of 10 species with an average value equal to an S2.

Examples of Extirpation Calculations for Groups of Co-evolved Species

We conclude this chapter by showing how the probabilistic methods described above apply to specific examples of co-evolved relationships, drawing specifically from the biodiversity found in North Carolina. We use two-species cases for the most part, since they are the easiest to display and discuss. However, we also demonstrate how ENE can be used to provide information for conservation purposes even for the largest and most complex of these groups.

Conditionally Independent Species