
Appendix 3.1

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1 Species characteristics and selectivity in extinction and speciation

Science has not ignored the roles of selective rates of speciation and extinction in the dynamics of species numbers and their contribution to the formation of patterns among species (exemplified by those presented in Chapter 2). Nonevolutionary factors seem to be better understood, accepted, and the focus of more research; however, selectivity at the species-level is of growing attention. It is useful here to provide access to a sampling of some of the literature in which we find consideration of the detail of selectivity in species-level dynamics with specific reference to species-level features thought to be subject to such selectivity. The objective is that of illustrating yet another aspect of science that is beyond our capacity to be exhaustive; the complexity of reality prevents our ever knowing all there is to know about the selectivity of either speciation or extinction. Does this amount to an argument to cease such studies? Absolutely not! We become convinced of the reality of such selectivity through such work. Such conviction will help substantiate in the minds of managers what scientists already know: selectivity occurs at multiple levels and is part of what contributes to the formation of integrative patterns, to be accounted for when these patterns are carefully used as the basis for management.

Thus, the following is far from an exhaustive account, but provides references and a brief treatment of related arguments for a sample of work

dealing with the study of selective extinction and speciation. Also included is a listing of factors and species-level features considered in regard to selective extinction and speciation beyond those treated in more detail in Chapter 2. In many cases numeric data are lacking for graphic presentation of frequency distributions or patterns. Much of the literature on extinction risk points to the cause-and-effect relationships between human activities and their contributions to the extinction that is occurring in today's world (e.g., Cardillo *et al.* 2004, Donazar *et al.* 2005, Fisher *et al.* 2003).

It must be emphasized that there are often synergistic effects among extinction risks making it difficult to see evidence for any one (e.g., Davies *et al.* 2004, Isaac and Cowlshaw 2004, Mattila *et al.* 2006, Owens and Bennett 2000). Thus, in cases wherein claims are made for a particular factor contributing to risk, it is often a risk identified through analysis in which other factors are taken into account through the statistical analysis used. Thus, "all else being equal" (which it never is), the factors identified as sources of extinction risk often function in conjunction with others to give rise to correlative patterns such as those covered in the latter sections of Chapter 2 where more than one dimension (species-level attribute) is involved simultaneously.

Small population size is a feature obviously associated with extinction risk (e.g., O'Grady *et al.* 2004). The volume of literature associated with this characteristic (well beyond being adequately treated here) provides a glimpse at what is in store for science focused on other species-level attributes. It is clearly a characteristic believed to contribute to the risk of extinction.

Another factor clearly accepted as a risk of extinction is reduced evolutionary plasticity. When faced with environmental change, species that

have limited capacity to change have less chance of survival than species that are more flexible (i.e., can evolve fast, Fowler and MacMahon 1982, Maynard Smith 1989, Pease *et al.* 1989). Generation time is a recognized component of evolutionary plasticity (Fowler and MacMahon 1982, Freeland 1986, Lenski *et al.* 1991, Marzluff and Dial 1991, Maynard Smith 1976a, Pimm and Gilpin 1989, Simpson 1953, Wilson and Willis 1975). Species with large body size have long generation times (Blueweiss *et al.* 1978, Fenchel 1974, Peters 1983) and limited capacity for change compared to species with small bodies and shorter generation times. Thus, extinction risk tends to increase with body size (Brook and Bowman 2005, Cardillo and Bromham 2001, Coe 1980, Davies *et al.* 2000, del Monte-Luna and Lluch-Belda 2003, Diamond 1984a,b, Fagan *et al.* 2001, Gage *et al.* 2004, Hallam and Miller 1988, Isaac and Cowlshaw 2004, Murray and Hose 2005, Owen-Smith 1988, Pimm *et al.* 1988, Raup 1986, Reynolds *et al.* 2005, Thomas *et al.* 2006, Van Valen 1973a,b, Vrba 1980, Wilcox 1980) so as to count among the factors causing the drop in species numbers with increasing body size (above an intermediate mode, Fig. 2.1). The extinction and speciation assumed as explanatory factors for observed macroecological patterns by Gaston and Blackburn (2000) relate to various life history characteristics, range size, and population variation as they are associated with body size (and clearly related to risk of extinction on their own). Cardillo *et al.* (2005) provide insight to the explanation of interacting factors behind the increased risk of extinction with increasing body size.

The maximum rate of increase per unit time (r_{\max} , in most literature on population biology) is a feature of species that is correlated with body size (Blueweiss *et al.* 1978, Peters 1983, Western 1979) and contributes to risk of extinction. Species with low rates of increase are also often (but not always) species with large body size and thus likely to experience elevated extinction risks relative to those with higher rates of increase (Dickerson and Robinson 1986). The higher rates of increase, themselves, are part of what contributes to evolutionary plasticity (Marzluff and Dial 1991). In the original analysis by Marzluff and Dial, a statistically significant relationship between extinction and fecundity

was not found. But their results were not consistent from group to group. The results presented in Table 1 of their paper show that only four out of 22 samples showed negative correlations—between -0.10 and -0.82 —which, nonparametrically, is statistically significant. Thus, as a statement for the overall sample (a sample of species), there is empirical basis for having shown a relationship between rate of increase (specifically fecundity) and extinction rates. All else being equal, extinction rates tend to be higher for species with lower rates of increase. This conclusion is supported by other work (e.g., Pimm and Gilpin 1989).

The rate of increase is the Malthusian capacity for increase that prevents extinction (Bateson 1972). As argued by Pimm *et al.* (1988), species with low rates of increase have a higher rate of extinction because of the extra time spent at low population levels following population decline. Modeling studies suggest that higher rates of increase carry less risk of extinction (Goodman 1987a,b). Richter-Dyn and Goel (1972) found that time to extinction (specifically for colonizing species) is related to birth rates. Marzluff and Dial (1991) argue that large intrinsic rates of increase reduce rates of extinction in part due to the capacity to expand the range and recolonize areas where local populations became extinct. Species with lower rates of increase are subject to higher risks of extinction in the face of hunting pressure (by humans, Price and Gittleman 2007). Species with large litter size tend to be less prone to extinction than species with smaller litters (Cardillo 2003). Johnson (2002) found the risk of extinction to be related to reproductive rate.

Evolutionary plasticity is one of the advantages of sexual reproduction (Emerson 1960, Ghiselin 1974, Lewontin 1957, Maynard Smith 1976a, Schultz 1977, Simpson 1953, Stanley 1975b, 1979, 1990a, Williams 1971). Thus, mode of reproduction serves as a simple example of the selectivity of both extinction and speciation (Fowler and MacMahon 1982, Maynard Smith 1978a, 1989, Stanley 1975b, 1979, 1990a). As Simpson and Beck (1965) summarize the matter (for species as populations in selective extinction and speciation, or subpopulations in group selection): “There is, therefore, no mystery attached to the nearly universal occurrence of sex in organisms. Those populations of

organisms most able to vary have been those most able to survive changing conditions in the environment and those most able to evolve new ways of life as the opportunities arose. Sex is widespread because, like any other adaptation, it has promoted the long-term survival of the populations having it". Like everything, however, there is another facet to sex: sexual selection is one of the factors under study in its contribution to evolutionary dead-ends (evolutionary suicide; Morrow and Fricke 2004, Morrow and Pitcher 2003).

Trophic level is another factor in the risk of extinction, in part because species at higher trophic levels suffer higher rates of extinction because of their dependency on species at lower levels (Fowler and MacMahon 1982). Empirical information has demonstrated that species at higher trophic levels are more vulnerable to extinction than their counterparts at lower levels (e.g., Purvis *et al.* 2000). Work related to these concepts is found in J. Brown (1971, 1981), Davies *et al.* (2000), Glazier (1987a), Marzluff and Dial (1991), Pagel *et al.* (1991), Patterson (1984), Petchey *et al.* (2004), Purvis *et al.* (2000), Terborgh (1974), and Wilson and Willis (1975).

Other forms of interdependence lead to extinction, the greater the dependence the higher the risk. Not surprisingly, the extinction of species exhibiting more interdependence has been observed to be higher than others that are less dependent. In particular, species showing symbiotic interdependence undergo extinction at higher rates than species without such strong dependence (e.g., Raup and Jablonski 1993, Rosen and Turnsek 1989).

Boulter *et al.* (1988) provide evidence that specialist species suffer high rates of extinction among plants when compared to less specialized species. Further evidence and basis for concluding that specialist species suffer high rates of extinction when compared to generalists are found in Anstey (1978), Davies *et al.* (2004), Davis (1990), Diamond (1976), Eldredge (1992), Futuyama and Moreno (1988), Geist (1978), Jablonski (1986a), Koh *et al.* (2004), Norton (1987), Patterson (1984), Paul (1988), Raup and Jablonski (1993), Ricklefs (1976), Rosen (1981), Simpson (1953), Stanley (1984), Unwin (1988), Vermeij (1983), Vrba (1992), and Watling and Donnelly (2007).

In terms of tolerance of environmental conditions, specialization may be related to geographic ranges. As indicated by Brasier (1988) and Gaston (1990), species that have broad ecological tolerance or use a wide variety of resources will also tend to have much broader distributions and be less likely to become extinct. Other considerations of the effects of specialization (especially habitat specialization) are found in Diamond (1984a), Dunn (2005), and Safi and Kerth (2004).

Specialization of various kinds has also been considered in regard to speciation (particularly cladogenesis, the splitting of a phyletic lineage to form two species; Gilinsky 1986, Vrba 1980, 1985).

Beyond intermediate levels, risk of extinction may increase with numbers of species consumed, through dynamics involving factors such as population instability, thus placing limits on how many species can be consumed. This combined with tendencies toward specialization through evolutionary changes contributes to limits on connectance observed in the field of food-web analysis (May 1972, McNaughton 1978).

Speciation rates are thought to vary with the extent of specialization as well as the positions in which species occur in trophic chains and symbiotic interactions. Evolutionary changes are expected among all species, including those at the first level in any such chain. Consumers of these resources are then faced with new circumstances and only those species that have the evolutionary plasticity to avoid extinction in tracking these evolutionary changes are expected to survive. Thus, species higher in such chains (or webs) of dependency would be expected to be characterized by increasing evolutionary plasticity and undergo more speciation than species upon which they depend. The idea of species evolving in reaction to each other in evolutionary systems (coevolution) is described or exemplified in the work of Benton (1987), Futuyama and Slatkin (1983a), Maynard Smith (1989), Raup (1988), Stenseth (1985), Stenseth and Maynard Smith (1984), and Van Valen (1973a) and often referred to as the Red Queen concept.¹ Coevolutionary ecology/biology (e.g., Thompson 2005) are fields of science devoted to the study of such interactions which involve evolutionary webs that permeate ecosystems and the biosphere as do food webs.

Species with small geographic ranges are more susceptible to extinction than species with larger ranges. Literature related to this conclusion includes island biogeographic work as well as work by paleontologists (e.g., Diamond 1984a, Gage *et al.* 2004, Gaston 1990, Gaston and Lawton 1990a, Glazier 1986, 1987b, Hanski 1982, Hope 1973, Jablonski 1987, Raup 1986, Rey 1984, Richman *et al.* 1988, Schoener and Schoener 1981, Scrutton 1988, Stanley 1989, Terborgh 1974, Terborgh and Winter 1980, Unwin 1988, Wilcox 1980). Species with large geographic ranges suffer the combined risks of increased numbers of species with which they interact and the potential of shear forces from diverging conditions in different areas to result in speciation (Glazier 1987b, Miller 1956, Rosenzweig 1995).

For population variability, the many explanatory processes contributing to the observed patterns include the risks of extinction associated with small population levels (J. Brown 1971, Crowell 1973, Dennis 1989, Dickerson and Robinson 1986, Goodman 1987a, Hallam and Miller 1988, Hull 1976, Karr 1982a,b, Pielou 1977, Raup 1986, Rey 1984, Richter-Dyn and Goel 1972, Simberloff and Abele 1974, and Terborgh and Winter 1980). Part of the risk of low population levels is that of Allee effects, wherein the slope of density dependence curves changes to be positive (depensatory) at low population levels. In extreme cases, the rate of population increase at low levels is negative and there is a tendency to decline to zero (Dennis 1982, 1989, Fowler and Baker 1991, Henle *et al.* 2004, Lande 1988, Mosimann 1958, Odum and Allee 1954). Papers that treat population variability, related selectivity in extinction, or provide more information on related patterns include Brown (1995), Connell and Sousa (1983), Diamond (1984a), Fowler and Baker (1991), Glazier (1986), Gaston and Lawton (1988a,b), Mosimann (1958), Pagel *et al.* (1991), Patterson (1984), Pimm *et al.* (1988), Schoener (1985).

Population variability can result from consumer/resource relationships in which the population level of the resource is reduced through the effects of consumption by the consumer. If such a resource species briefly escapes the effect of predation, it can grow to large population size, thus stimulating growth and higher consumption by the consumer and then experience a resulting

population crash. Species that exhibit significant reduction in their resource species count among keystone species (Mills *et al.* 1993, Paine 1966, Roughgarden 1983). But, as explained, these circumstance can give rise to population fluctuation in which the magnitude of the fluctuations is related to the degree the resource species is (are) reduced by the consumer (May 1973, 1981a). Thus, one of the contributing factors in the drop in species numbers with increasing interaction strength may relate to the risk of extinction from any resulting population variability. Jonsson *et al.* (2006) found interaction strength to be a source of extinction risk in model systems.

The kind and level of density dependence that species exhibit in their populations is related to risk of extinction (Henle *et al.* 2004). With no density dependence a species is doomed to extinction (Bateson 1972, Ginzburg *et al.* 1990, Royama 1977, Whittaker 1975). Quoting Whittaker: "In principle, a population that randomly walks in time, without some density-dependent limitations, must walk randomly to extinction. In this view, density-independent population control is a contradiction in concepts. Influences limiting fluctuation are necessary to the long-term survival of populations". According to Godfray and Hassell (1992): "It is a logical necessity that any population of plants or animals that persists in the environment must experience some form of density-dependent feedback on population growth...". For further treatment of this argument see Brown (1995), Godfray and Hassell (1992), Hanski (1990), Hanski *et al.* (1993), and Shepherd and Cushing (1990). As Hanski *et al.* (1993), Holyoak and Lawton (1992), Royama (1977), and Woiwod and Hanski (1992) argue, with time and increased sampling, it is expected that virtually all species will be shown to have some degree of density dependence. This conclusion is based in large part on the argument that species without, or with low levels of, density dependence suffer high extinction rates that are much higher than for species that show density dependence. However, at extreme levels of density dependence, populations run a higher risk of cyclic or chaotic behavior (Ginzburg *et al.* 1990, May 1975) and the risk of extinction associated with high population variability mentioned above.

Evidence of the advantages of mobility in reducing the risk of extinction is far from rare in the scientific literature as seen in Diamond (1984a), Dickerson and Robinson (1986), Eriksson and Bremer (1991), Farnworth and Golley (1974), Janzen (1983), Marzluff and Dial (1991), Norton (1987), Owen-Smith (1988), Pimm *et al.* (1988), Raup (1986), Reinhardt *et al.* (2005), Terborgh (1974), Van Valen (1971), and Wilcox (1980). Unwin (1988) indicates that the birds of today are the principle descending survivors of the dinosaurs owing at least in part to their mobility. As indicated by Eldredge (1991), organisms that fly, swim, walk, or have their seeds carried to a new habitat can avoid changes caused by shifts in their habitat owing to climatic changes over evolutionary time. As pointed out by Davis (1990) and Roberts (1989) the survivors of the extinction processes involve many with insured seed dispersal as a means for the species to relocate during times of environmental change. Knoll (1984) also presents information and arguments indicating that plant species that have effective dispersal mechanisms survive periods of changing climate better than those that do not. Bats may be much more numerous as species than other mammals of the same size because of their mobility.

Selectivity at the species level is frequently mentioned for a variety of factors beyond those mentioned above. Very few are represented by graphic illustrations of related patterns. The examples in the following paragraphs are presented here as a means to make the points that (1) in the end, the complexity of reality is such that we, as scientists, can never hope to find, account for, or understand all such factors, especially in their combination(s) (see Table 2.1), (2) there is a rich opportunity for science working on these matters to further substantiate what managers must know: selective extinction and speciation count among the factors that result in patterns that we see, and (3) the patterns we see provide information that accounts for such factors (including those we have yet to discover) when we use the resulting patterns in management.

Behavior (including communication, social organization) has been seen as a factor in selectivity at the species level (Glazier 1987a, Munoz-Duran 2002). The biochemical composition of species show patterns (e.g., Woodward 1993) that may be partially explained by differential extinction, as

would be patterns in decomposition. The energetic or thermodynamic patterns in communities, ecosystems, and the biosphere are subject to a great deal of research involving microevolution and the interactions among both individual organisms and species. These, more conventional, kinds of research are being joined by work on selectivity at the species level that also contributes to observed patterns (Brown 1995, Damuth 1981, 2007, Fisher 1986, Jørgensen 1992, May 1981b). The amount, kinds, and variation of genetic material (see polyploidy below) are observed to fall in patterns (Ayala 1978, Beardmore 1983, Fisher 1986, Fowler and MacMahon 1982, Holland *et al.* 1982, May 1978, Raup and Jablonski 1986) that involve selectivity, not only at the chemical and individual levels, but also at the species-level. In addition to specialization measured in terms of resource specialization, habitat association and utilization involves specialization that is likely subject to selectivity in both extinction and speciation (e.g., Schoenly *et al.* 1991).

Interaction strength (e.g., rates of consumption of resource species) involves more than population level effects. They also involve the intensity of any selectivity involved to result in "coevolutionary intensity" as an interaction of varying magnitude that undoubtedly lends itself to varying probabilities of either extinction or speciation (Jordano 1987). In addition to the life history traits of rates of increase, ages at first reproduction, and mortality schedules, there are species with morphological and developmental stages, and behavioral patterns such as dormancy, also subject to species-level selectivity (Bush 1975, Carlquist 1965, Cristoffer 1990, Dial and Marzluff 1989, Diamond 1974, Glazier 1980, 1987a, Herrera 1992, Jablonski and Lutz 1983, Marzluff and Dial 1991, May 1978, Maynard Smith 1989, McKinney 1990, Mertz 1971, Scheiner 1992, Spicer 1989, Stearns 1992, Sukopp and Trepl 1987, Upchurch 1989). Mimicry and chemical communication signals count among factors thought to be important at the species-level (Gilbert 1980, 1983).

One of the more clearly established patterns thought to be important in selective extinction and speciation are the elements of mobility and dispersal (Brown 1995, Eldredge 1991, Gilinsky 1986, Glazier 1980, 1986, 1987a, Jablonski 1986b, 1989, Jablonski and Lutz 1983, Marzluff and Dial 1991, Pacala 1989,

Raup and Jablonski 1986, Stanley 1990a, Sukopp and Trepl 1987, Vermeij 1987, Wilcox 1980). In the category of behavior are specific modes of feeding or nutrient uptake thought to be subject to species-level selectivity (Jablonski 1989, McKinney 1990, Murray 1984, Patterson 1984, Paul 1988, Raup and Boyajian 1988) as are various sensory perceptions of the environment (e.g., visual, auditory, thermal; Fisher 1986). Phenotypic plasticity helps avoid genetic rigidity and lends to species-level advantages much as does evolutionary plasticity—a kind of genetically derived plasticity to mitigate for evolutionary inflexibility (Hoffman 1983, Pacala 1989, Parsons 1991a,b).

Even the amount of genetic material shows patterns among species, initially seen in the polyploidy measured for various species (Ehrlich and Wilson 1991, Gibby 1981, Masterson 1994, Orr 1990, Rosenzweig 1974, 1975, 1995) and potentially subject to differential speciation and extinction rates. Not unrelated would be the matter of genetic variation (Lloyd and Gould 1993). In addition to the patterns in lifetime reproductive effort (Charnov *et al.* 2007), there may be patterns in production efficiency (May 1981b) that contribute to the changes of species-level success or failure. Both of these factors involve reproductive and mating systems which are not independent of interspecific factors such as pollination (and its concomitant interdependence, risks of extinction, and contributions to speciation) (Barrett 1989, Bond 1995, Branch 1984, Dobson and Lyles 1989, Donoghue 1989, Gill 1989, Glazier 1987a, Herrera 1992, Lieberman and Vrba 1995, Maynard Smith 1989, Orians and Kunin 1990, Sukopp and Trepl 1987).

Finally, much as one might see the risk of death being associated with immaturity among individual humans (as well as individuals for most species), it appears that the age of a species is related to its risk of extinction. Age or “experience” seems to count among species as well as among individuals (Boyajian 1991, Herrera 1992, Orians and Kunin 1990).

Notes

1. Van Valen (1973a) described the process of species evolving in response to each other’s evolution by quoting from L. Carroll’s “Through the Looking Glass” (“Now

here, you see, it takes all the running you can do, to keep in the same place”). Such processes are thus termed the Red Queen model of evolution (Maynard Smith 1988).

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