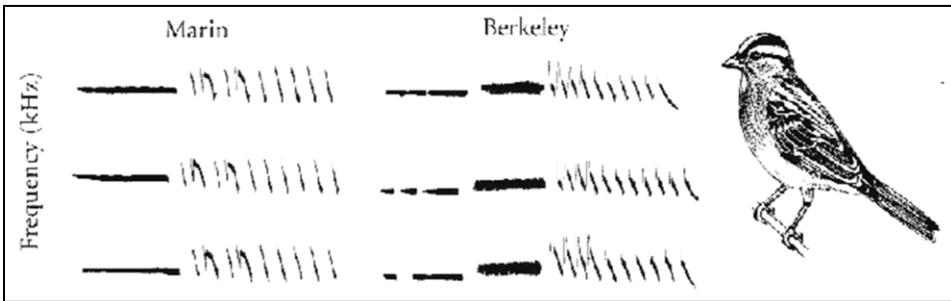


NOW, on to an introduction to MACROEVOLUTION – how diversity of populations and species arises.

FIRST: It shouldn't be surprising that allopatric populations of many species diverge to some degree. Local 'types' might be called races, subspecies, and differences among them could be due to differences in selective environment OR to chance differences in the course of genetic change over time. If the regional types show specific local adaptations, they're often referred to as *ecotypes*.

The physical separation of populations can play an important role in their divergence; if there is no physical separation, there can always be mating and exchange of genes across continuous range (this is called 'gene flow'). Physical separation – allopatry – can allow selection to 'shape' local populations in without variations being 'swamped' by gene flow.

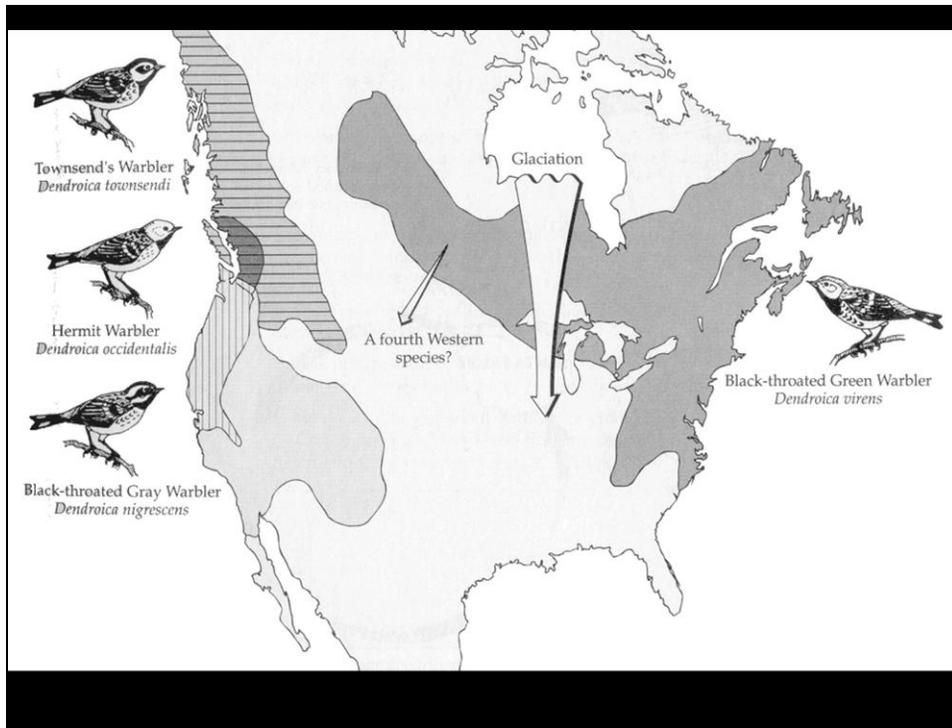


Song dialect patterns in white-crowned sparrows (*Zonotrichia*)

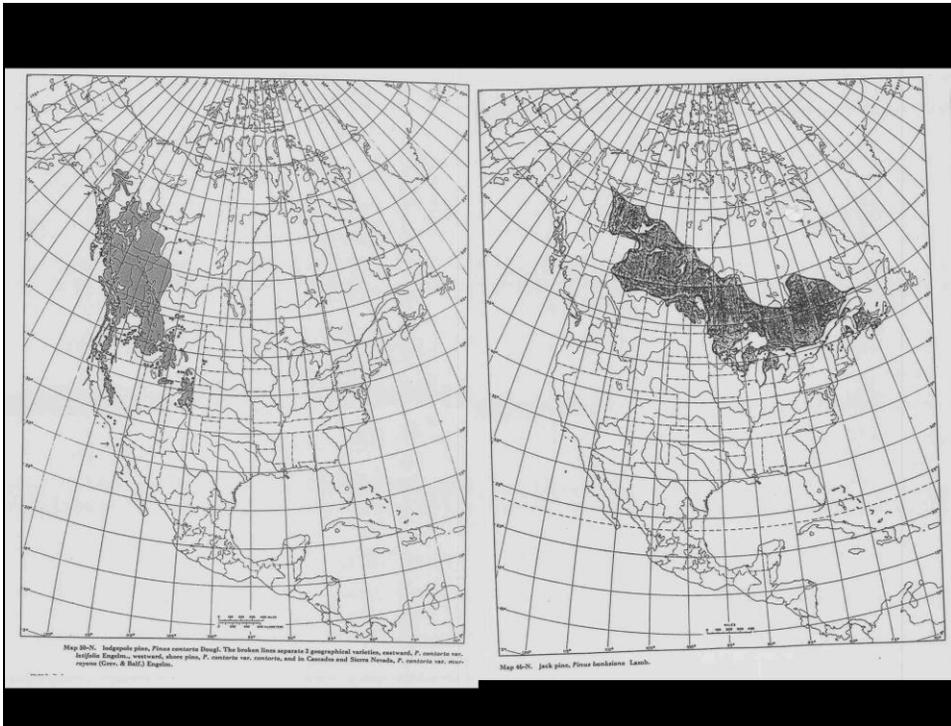
White-crowned sparrow (*Zonotrichia leucophrys*) songs are used in male territorial displays, and vary across short distances. The sonograms show frequency against time for three individuals from each of two populations in Northern California. The Berkeley dialect is a rising two-note call followed by a trailing trill, the Marin dialect is a single note followed by a steady trill. Song dialects appeared to be learned.
 (after Jonsson 1992; from Futuyma 1998).



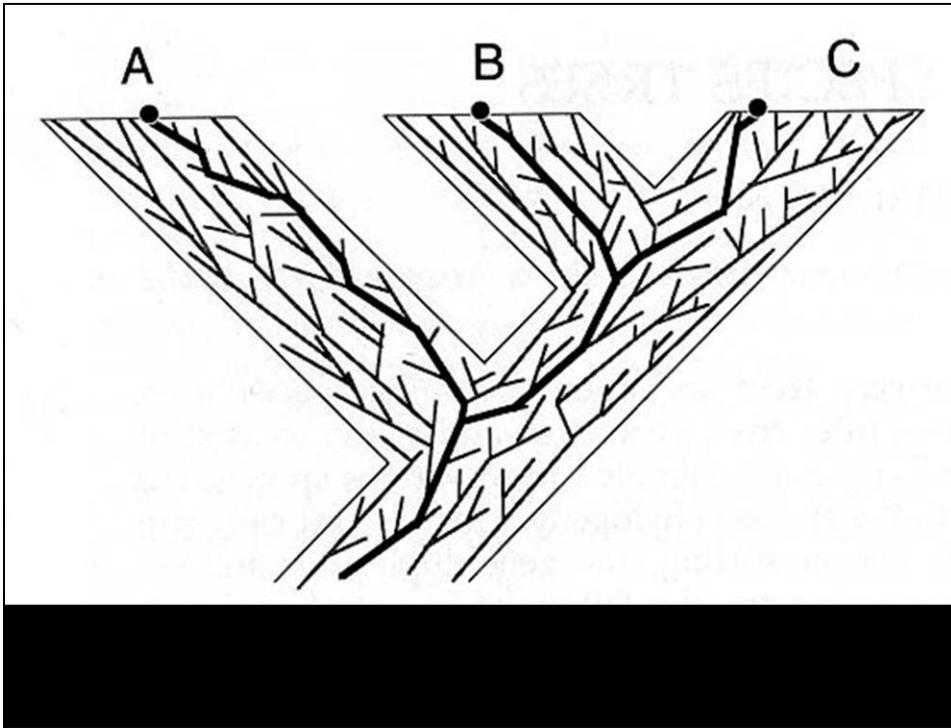
Lots of examples; two regional subspecies of spotted owl. There are differences in coloration and habits, but they're still placed in same species *because there's reason to think they'd interbreed pretty freely if brought into contact* (and remember that one significant part of the admittedly muddy 'species concept' is the notion of *separate gene pools* – genetic isolation.



But what if, in allopatry, the differences between regional populations become so pronounced that they DON'T interbreed if brought back into contact? Here, imagine a new glaciation splitting the range of the common and wide-spread black-throated green warbler into separate western and eastern groups. Then, after 100,000 years, the glacier retreats, allowing the two 'sibling' groups to come back into contact. Would they have become sufficiently different that they wouldn't recognize each other as potential mates? Would behavior have changed so that they'd no longer even come in contact? In such a case, we'd have to treat them now as separate species (we'd call them 'sibling species' because they have a recent common ancestor). This process is referred to as speciation – the splitting of one species into two. In this case, it would be *allopatric speciation* – divergence happening while ranges physically separated. Allopatric speciation is probably the most important form of speciation – the means by which most species diversity has been created.



Here's a similar story with lodgepole pine (western) and jack pine (eastern). They've always been considered sibling species, but two genuinely distinct species. However, where their ranges have come back into contact (northwestern Alberta and surrounding areas), they appear to be hybridizing rather freely. Maybe we'll have to reconsider and treat them as races or subspecies of a single species. The process of speciation can be a little ambiguous.



As in this conceptual diagram, where the vertical axis is time, the horizontal represents differentiation in some phenotypic ‘space’. The solid branching lines can be thought of as sub-populations and their lineages. Some go extinct, some persist, some give rise to distinct ‘daughter’ sub-populations. At the present (top), these lineages exist in three relatively distinct groupings – we might call them species A, B, and C. But it might have been unclear, in the relatively recent past, whether to treat the ancestors of B and C as separate groups or just a single highly variable one.



American black duck

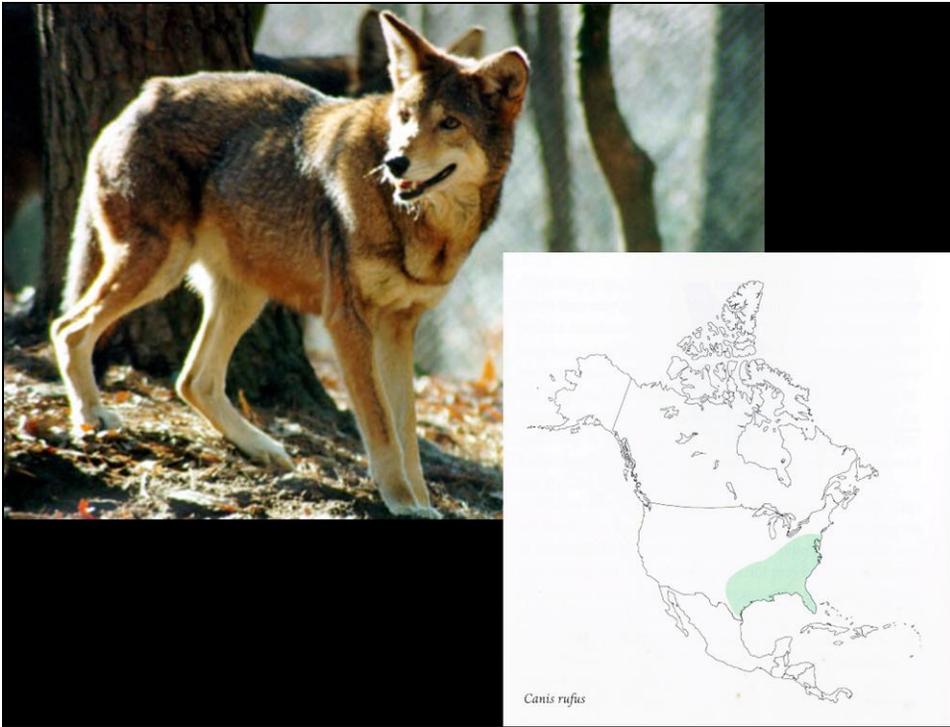


Hybrid and mallard

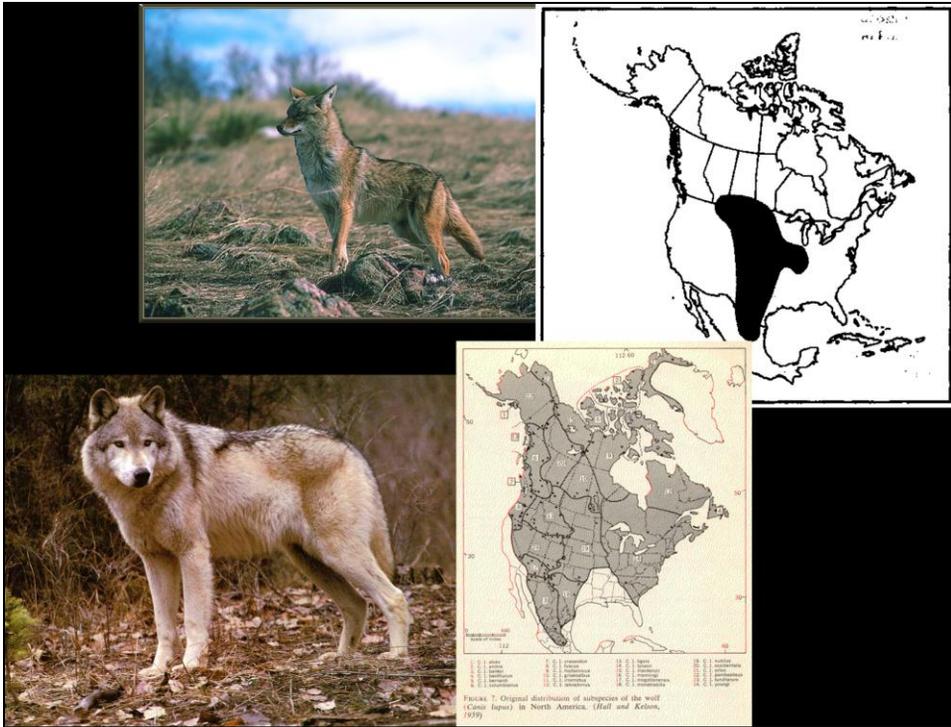


Mallard

Black ducks and mallards are sibling groups that used to be thought of as allopatric species. They've come into contact with one another, and hybridize freely (because mallards are more abundant, their gene pool is swamping that of the black duck). The speciation process was incomplete.



The 'red wolf' of the southeastern U.S. appears to be a population originating from hybridizations of:

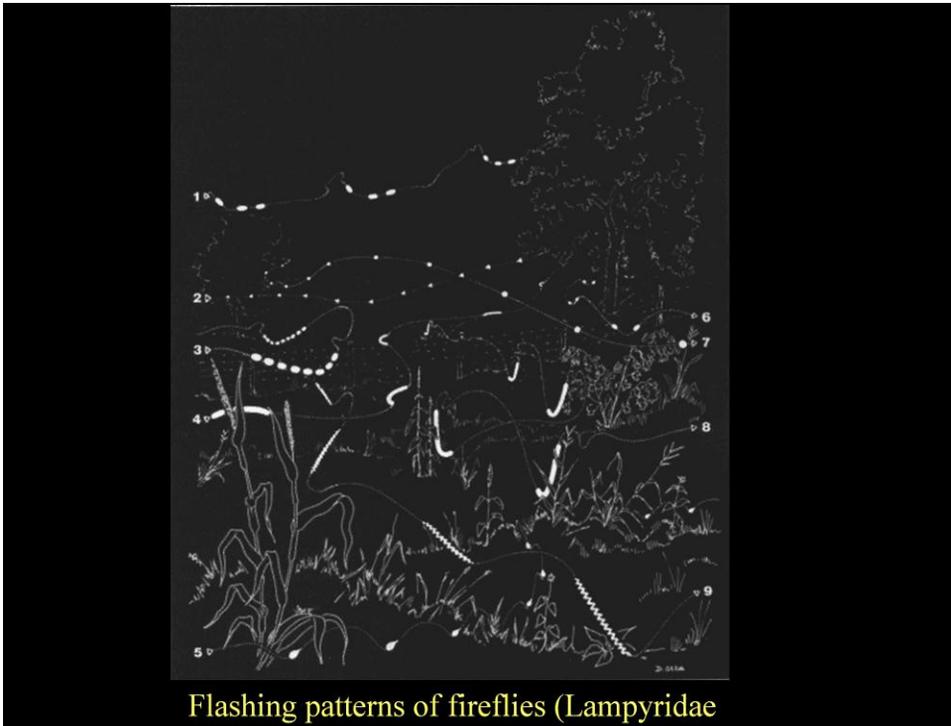


Timber wolves (bottom), which were historically very wide-ranging, but which were exterminated from eastern U.S., and coyotes (top), historically a species of the great plains, but who've spread eastward with changes in the landscape and elimination of wolves. Presumably, at some point when one or both were rare enough in the southeast so that mates were hard to find, some wolf (or wolves) mated with coyotes rather than eating them.

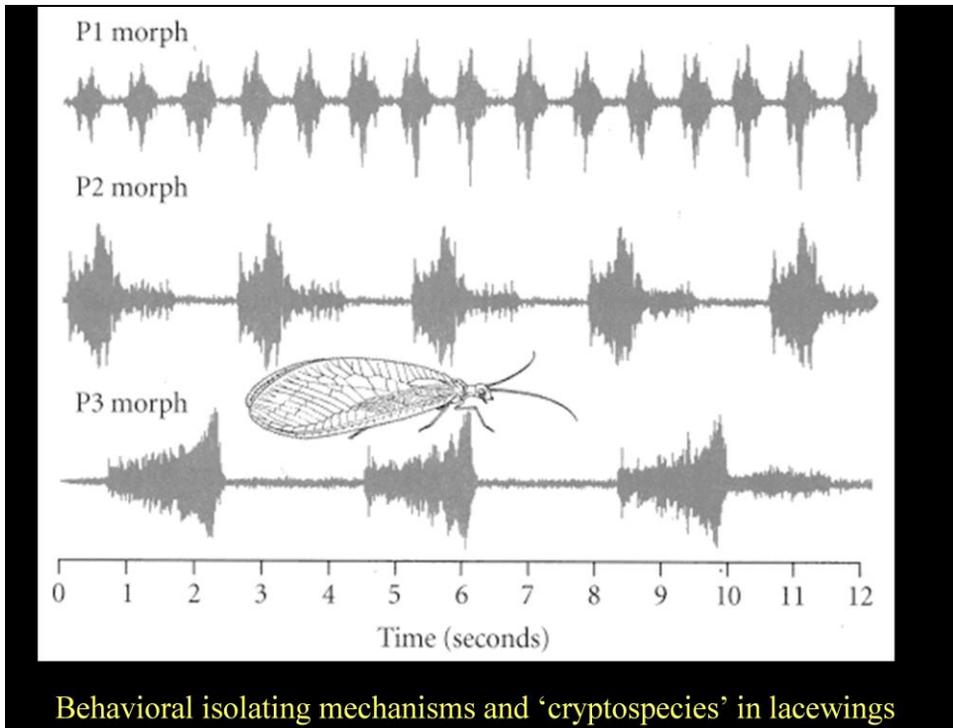


Larus argentatus complex: Argentatus subsp A, B, and C apparently evolved as Pleistocene isolates. D = separate species (*L. glaucoides*) that evolved in North America. After Pleistocene, subsp A spread across N. America into Europe where sympatric with subspecies B, from which it remains distinct. = "Rassenkreis" or "race circle". (From Mayr 1963)

“Ring species” are a strange situation, but not uncommon. Here, a group of ‘types’ of gulls are shown. Each geographical variety interbreeds with adjacent varieties where their ranges come in contact. EXCEPT types A and B where they overlap (are sympatric) in northern Europe; they don’t interbreed there at all. But both can pass genes through intermediate types in Asia to end up in the ‘other species’ where they’re sympatric! They don’t care what we call them or whether they fit in our species concept...



BUT, ultimately, divergent branches from a common ancestry may become so different that there's no longer gene flow. We say that there's an effective REPRODUCTIVE ISOLATING MECHANISM (RIM). THEN they're 'good species'. Here, the RIM is the pattern of flashes by which female fireflies choose males; each species has (and chooses) a distinctive flash pattern. Even if they were genetically compatible, they are reproductively isolated by mate choice.



And even some species that LOOK almost identical may, in fact, be fully isolated by such mechanisms...