PER Take Home Exam #1: KEY

This key represents one complete solution set (indeed, question 1 is answered "more than" fully); because we asked for examples, it is unlikely that anyone's test will look exactly like this one. I have provided appropriate examples here, but for every parameters or evolutionary concept, there are many correct examples.

1. What parameters increase the likelihood that an introduced species will turn into an invasive species? Identify at least five distinct factors, and supply specific examples that were not discussed in class to support these.

i. If the "natural enemies" hypothesis (aka enemy release hypothesis) is true for this species in this environment, that suggests that the suite of competitors and predators/herbivores that the introduced species would be struggling with in its native environment is not present in its new environment. This should allow it to outcompete and/or outgrow those species that would be competing for the same niche in the new environment.

Example: On the Great Plains of eastern Montana, Russian olive and tamarisk are introduced woody plants, while cottonwood (trees) and beavers are native. In those areas where all four species co-exist, beavers preferentially fell cottonwood trees (>80% of all individuals in a plot), while rarely touching the introduced plants. This provides a competitive advantage to both introduced species. (Source: Lesica, P. and S. Miles. 2004. Beavers indirectly enhance the growth of Russian olive and tamarisk along eastern Montana Rivers. Western North American Naturalist 64(1): 93-100.)

ii. If the hypothesis of allelopathic advantage is true (for this species in this environment), the newly introduced species is predicted to poison its would-be competitors, whereas in its native environment, its competitors have presumably evolved defenses against such toxins.

Example: In Norwegian sub-alpine forests, two native spruce species (*Abies spp.*) are harvested for lumber, but do not regenerate as quickly as would be expected given their dominance in undisturbed habitats. Presence of introduced bilberry (*Vaccinium myrtillus*) is correlated with low germination rates of Norway spruce. Phenolic acids are produced by bilberry and found at high levels in soil where bilberry is present, and have been found to inhibit seed germination in Norway spruce (Mallik, A. U. and F. Pellissier. 2000. Effects of *Vaccinium myrtillus* on Spruce Regeneration: Testing the Notion of Coevolutionary Significance of Allelopathy. Journal of Chemical Ecology 26 (9): 2197-2209.)

iii. The "evolution of increased ability" hypothesis is a stretch for this answer, as you cannot know in advance if a particular species has a capability that will allow out to take the "natural enemies" hypothesis this one step further, and use those resources that it is not shunting to competition or predator defense for "additional ability." However, a careful argument, with the appropriate example, could be made for this.

Example: I did not track down a good example of this.

iv. Islands: are more likely to be invasible because their inhabitants typically have reduced competitive ability (smaller size, reduction in flight capability in winged animals, fewer resources put to defensive structures), due to the reduced species richness on islands. (Thus, islands may be invasible for reasons related to the natural enemies hypothesis.) Exceptions to this include easily-dispersed species (e.g. wind-dispersed plants such as grasses), or easily dispersed-to islands (such as those that are close to source populations physically, or effectively close due to tradewinds and/or ocean currents).

Example: There are many good examples of islands having been invaded by non-native species. One is of insects on the Galapagos Islands: of 463 known insect species introductions, 6 are known to be invasive, and another 52 species are predicted to be highly invasive, putting native populations of both insects and plants (as most of these insects are herbivorous) at risk. (Source: Causton *et al.* 2006. Alien insects: Threats and implications for conservation of Galapagos Islands. Annals of the Entomological Society of America 99(1): 121-143.)

v. Highly disturbed landscapes will increase the invasibility of almost any species brought in (Note that this is a feature of the ecosystem, rather than the species.)

Example: Comparisons were made of species richness and abundance (of birds, small mammals, and lizards) in Madagascan spiny forest and adjacent plots that had recently been cleared ("disturbed" regime). Intact spiny forest has very high rates of endemism, with low invasibility. Cleared areas had higher rates of both introduced species and generalist species. (Source: Scott et al. 2006. The impacts of forest clearance on lizard, small mammal and bird communities in the arid spiny forest, southern Madagascar. Biological Conservation 127(1): 72-87.)

vi. High numbers of or repeated introductions of a species.

Example: There are, alas, almost infinite examples of this.

vii. The species is being introduced into an ecosystem of similar broad type (e.g. latitude, altitude, diversity, dominant growth form) to which it is native.

Example: Two congeneric butterfly species (*Erebia spp.*) in the mountains of the Czech Republic are able to disperse, and thereafter invade, new habitats that are most similar to their native habitats—notably in aspects of altitude, and habitat type (woodland vs. subalpine grassland). (Source: Cizek *et al.* 2003. Vacant niche in alpine habitat: the case of an introduced population of the butterfly *Erebia epiphron* in the Krkonose Mountains. Acta Oecologica 24(1): 15-23.)

Other acceptable answers that we saw on tests include:

- All else being equal, any phenotypic character which provides a competitive advantage, or reduces generation time, will provide an introduced species an advantage. Such characters might include faster growth, larger clutch size, or shorter generation time. The caveat here is that all else is rarely equal. Still, congeners (that is, very closely related species) that were otherwise identical, one of which had shorter time to reproductive maturity, would likely outcompete the other. This is likely to be true only for closely related species, however (due to the "all else being equal" clause).
- Under appropriate conditions, generalists are likely to be more invasive than specialists. The critical caveat here is "under the appropriate conditions." Simply identifying "generalist" is not quite sufficient, although it often will be sufficient because many habitats have other parameters which, in combination with the introduced species being a generalist, makes them invasible. These parameters

include some of the other parameters already mentioned, including being an island, already being disturbed, and also being in a temperate climate (generalists don't have a leg up in the tropics where the many niches are already well populated by specialists).

2. Define each of the following concepts, and for each, identify a particular issue in modern human health that can be better understood by applying the concept, using the basic premises of evolutionary medicine. Be as specific as possible, and use examples other than those from lecture. You may want to refer to one or more of the changes that have occurred in the last 5 mya in how humans interact with and use their environment. Of the three examples that you provide, which one seems the most intractable (that is, most difficult to cure or resolve), and why?

a) Adaptive landscape: a conceptual framework (not reality) which is a surface that describes that subset of design space that is physically, chemically, and biologically possible, given a particular environment. High peaks represent maximally adaptive phenotypes, but organisms/populations cannot attain high peaks if they happen to exist on the slopes of a lower one, because selection (like gravity pushing air bubbles up under a sheet of ice) acts only in the moment, and it can thus only move an organism/population "up slope" of whatever peak it was on. Thus, it is not the relative height (adaptiveness) of the peaks which predicts where a population will end up, but rather the depth of the valleys (lack of adaptiveness?) between those peaks. This concept of global and local maxima is critical in understanding the effects of changing environments on organisms' fitness as well.

Example: In the Environment of Evolutionary Adaptiveness (EEA), women had far fewer ovulatory cycles than in the modern environment, due to several factors including but not limited to:

- more caloric intake now (therefore earlier onset and later offset (menopause) of menses. Due to advent of agriculture, then the industrial revolution.)
- lower birthrate now (therefore fewer months of both gestation and lactation → more months of ovulation; due to decreases in child mortality and increases in women's emancipation. Remember the naturalistic fallacy, however, and do not blame the women's movement; a nod, here, to newly departed Betty Friedan, founder of feminism's second wave.)
- lower rates, and shorter duration of, breast-feeding (due to the advent of, first, wet-nurses, and now, synthetic alternatives in combination with changing cultural mores).

All of which contribute to many more ovulation cycles in modern women than women in the EEA had, which is correlated with an increase in the risk of many cancers. Correlation of reproductive cancers with high rates of ovulation was "invisible" to selection when ovulation was the exception, rather than the rule, for women. As the adaptive landscape has shifted with cultural evolution, we find ourselves on a less-adapted peak than we were previously, but selection cannot act to save us from ourselves.

b) Red Queen: a reference to any arms race between two evolved, responsive players, e.g. prey and predator, or host and pathogen. Both players are constantly adapting (running) just in order to stay in the same place, relative to their opponent.

Example: HIV, or any retrovirus that attacks humans. All viruses are engaged in a Red Queen-style arms race with their hosts. But retroviruses (that is: viruses made of single-stranded RNA, rather than the "usual" double-stranded DNA) have a particular advantage, as they can evolve more quickly. In brief: The double-stranded nature of DNA provides error correction in replication—if a nitrogenous base mutates, its complement (the other half of the "base pair") will not be able to match up with it, and the error with be detected. When RNA, which is a single-strand of nitrogenous bases, replicates, there is no such error correction, so mutations occur at a much higher rate. Most mutations, as always, are deleterious, but some are not, and this allows for HIV, like all retroviruses, to evolve at a much faster rate than if they were DNA viruses. This means that our efforts at developing effective anti-retro-virals will likely never end—for what is effective for today's HIV may not be effective for the HIV of 2007.

c) Historical constraint: Because of the long evolutionary history of a lineage, an organism's current form may not immediately (or possibly ever) be transferable into a different form.

Example: The human appendix. The appendix was, in our evolutionary past, a portion of the caecum, but no longer has the function of a caecum (that is: digesting plant fibers, or cellulose). While there are some who argue for a modern immunological function of the appendix, most researchers agree that the appendix, today, is a remnant of our past (as evidenced by the fact that all the apes, including humans, have a non-functional appendix) that can rupture and cause health problems, but does not provide benefits.

Of these three examples (risks of cancer from high ovulation rates, high rates of mutation in retroviruses such as HIV, and risks from burst appendixes (appendices?), the problem of retroviruses is the most intractable. Indeed, for most examples that you might come up that represent these three concepts, it will usually be the arms-races that provide us with the least solvable dilemmas. Recognition of the fluidity of adaptive landscapes, and of the rigidity of historical constraint, can help us modify behaviors and develop medical techniques or procedures to help deal with those problems. But arms-races are just that, and it is rare that we "win" such a race; rather, we will continue to run as fast as we can, to stay in relatively the same place.

3. Smil documents an ongoing transition from "traditional" to "fossil fuel" civilization. In readings and lecture we have explored some of the potential limits to this new phase in human development. Compare the transition from fossil fuels to the transition to them. What are some of the similarities and differences? Be as precise and specific as you can, making reference to the ideas and information we have been considering. You may want to take into account the social and biophysical causes of these transitions, the mechanisms through which they occur, their consequences for human beings and their relationship to natural processes. Do not feel as though you have to say everything; a few well-established points will be sufficient.

Similarities:

Fossil (F) and post-fossil (PF) fuels all derive from the two fundamental energy sources, solar radiation (mostly) and geothermal energy (a little). F represents solar energy stored as biomass and then compressed through geological processes. PF may be biomass (biofuels) or indirect products of solar radiation, such as wind. This could also be thought of as a difference, however: F taps the stock of previously emitted energy, whereas PF (except for uranium) is limited to the current flow.

F and PF sources of energy represent extensions of the human ability to do work. They are limited by conversion efficiencies from initial source to end use. But there is also a crucial difference: transition to F above all expanded the energy resources available to human beings. Even rather large inefficiencies in conversion have been tolerated because the throughput has been so large. Transition from F will entail higher efficiencies in both conversion and the amount of work (in the physical sense) required to accomplish human goals. (We will need much greater fuel efficiency in our vehicles to shift to biofuels, and we will need less automobile and truck use to achieve the needs of personal mobility and shipping.)

Differences:

The transition to PF will be largely determined by the cost and availability of F. This is because the energy densities of F range from high to very high—higher than PF alternatives, except perhaps for nuclear. (This is if nuclear proves to be a PF.) Transition to F was largely independent of pre-F sources: it occurred in timber-rich US and timber-poor England, etc. Cost and availability of resources like oil, coal and natural gas are modeled by rent theory (which envisions increasingly poor reserves entering the market) and the Hotelling backstop hypothesis (which carries future scarcity forward into current prices). Geopolitical uncertainties may further impinge on availability.

The transition to F has been occurring over a period of hundreds of years, from the emergence of coal technology in England in the 18th c. to the ongoing transition in developing countries today. Transition from F will almost certainly take place in a shorter time frame, with less opportunity for technological coevolution. Transition from petroleum, in particular, might have to take place in just a few years. Smil documents how an important series of innovations, from the steam engine to the steam turbine, internal combustion engine and electric motor, made it possible for human society to derive more benefit from F. We face the challenge of transitioning to new energy sources with less opportunity to co-develop new ways to convert and apply them.