J. Baird Callicott, ed., *Companion to A Sand County Almanac: Interpretive and Critical Essays.*
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12 ✶ Duties to Ecosystems

HOLMES ROLSTON, III

"A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise" (224-25).

"That land is a community is the basic concept of ecology, but that land is to be loved and respected is an cxtension of ethics" viii-ix).

"'The plant formation is an organic unit . . . a complex organism." [1] So Frederic Clements, a founder of ecology, concluded from his studies in the Nebraska grasslands. Henry Gleason, a botanist of equal rank, protested, "Far from being an organism, an association is merely the fortuitous juxtaposition of plants."[2] Leopold takes a middle: route between these extremes.[3] The ecosystem is a "biotic community." Moreover, moving from what *is* the case to what *ought* to be, Leopold argues a land ethic, duties toward ecosystems.[4]

Clements' description has seemed implausible to most ecologists, but if correct, duties to a superorganism could plausibly follow, since ethics has classically felt some respect for orga· nismic lives. Gleason's description has seemed as simplistic as Clements' is overdone, but if correct, duties to ecosystems would vanish. There: can be no obligations to a fortuitous juxtaposition. What Leopold's biotic community? Most ecologists have coordinated thought that an ecosystem was a real natural unit, a level of organization above its member organisms.[5] Is the de· scription plausible? Do prescriptions follow?

John Passmore, a philosopher entering the argument, thinks that only paradigmatic human communities generate obligations. "Ecologically, no doubt, men form a community with

plants, animals, soil, in the sense that a particular life-cycle will involve all four of them. But if it *is* essential to a community that the members of it have common interests and recognize mutual obligations, then men, plants, animals, and soil do *not* form a community. Bacteria and men do not recognize mutual obligations, nor do they have common interests. In the only sense in which belonging to a community generates ethical obligations, they do not belong to the same community."[6] Passmore is assuming that the members of a morally bound community must recognize reciprocal obligations. If the *only* communal belonging that generates obligations is this social sense, involving mutual recognition of interests, then the human community *is* the sole matrix of morality, and the case is closed. We owe nothing to nonhumans, much less to ecosystems. But Leopold wants to open the question. Passmore thinks closed. Extending the logic of ethics beyond culture, can mutually recognized obligations and interests be replaced by respect and love for ecosystemic integrity, stability, and beauty? Can a community per se count morally?

A first consideration is that the organism is a model of cooperation while the alleged ecosystemic "community" seems a jungle where the fittest survive. Fully functioning persons can be expected to cooperate in the deliberate sense, and interhuman ethics has admired being kind, doing as you would have others do to you, mutually recognizing rights, or calculating the greatest good for the greatest number. But symmetrical reciprocity drops out when moral agents encounter amoral plants and animals. To look for considerate cooperation in the biotic community is a category mistake, expecting there what *is* only a characteristic of culture.

But at least nondeliberate *cooperation* is an admirable feature in organisms, who seem to command ethical respect because, from the skin in, they are models of coaction. The heart cooperates with the liver, muscles with the brain, leaves with the cambium, mitochondria with the nucleus. Life is contained within individualized organisms, notwithstanding colonial species, slime molds,

and other minor exceptions. Respect for life, therefore, ought to attach to individuals, where the "integrity, stability, and beauty" is.

From the skin out, everything is different. Interactions between individuals are nothing but *struggle*. Each is out for itself, pitted against others. Carnivores kill herbivores, who consume the grasses and forbs. Young pines smother each other out. Black walnuts and *Salvia* shrubs secrete allelopathic agents that poison other plants. Apparent harmony in ecosystems is superficial. Chokecherries benefit redwing blackbirds, but the fruits are bait and a gamble in reproductive struggle. Neither plants nor animals are moral agents, and to regard carnivore or *Salvia* behavior as "selfishness" is a mistake, just as much as to expect deliberate cooperation. We are not faulting organisms. Still, the organism is parts admirably integrated into a whole. The ecosystem is pulling and hauling between rivals, no admirable community. To adapt Garrett Hardin's phrase, there is tragedy on the commons.

Such a picture accentuates the skin-in cooperation and the skin-out conflict. Ecology refocuses both the description and the resulting prescription. The requirement that parts in wholes "help each other out"—charitably in culture and functionally in nature—makes another category mistake, trying to assimilate to civilization what needs to be admired in wild nature. Were cooperation the criterion, we would admire the elephant's heart and liver, and even admire the integrated whole elephant, only to despise the elephant's behavior, since the integrated elephant-unit consumes all the bamboo and acacia it can and tramples the rest of the gallery forest in majestic indifference. The elephant is coordinated within to struggle without, and would-be admirers are left ambivalent about individuals. The individual is an aggrandizing unit as much as a cooperative one. Such units propel the ecosystem.

The deeper problem seems to lie in the axiom that everything is pushing to maximize itself, with no further determining forces. In fact, although aggrandizing units propel the ecosystem, the system limits such behavior; there is a sufficient but contained place for all the members. Imposed on organisms from the upper organizational level (if indeed each species in-

creases until "stopped") this containment can seem more admirable than the aggressive individual units. The system forces what cooperation there is, embedding every individual deeply in coaction.

What we want to admire in nature, whether in individuals or ecosystems, arc the vital productive processes, not cooperation as against conflict, and ethicists will go astray if they require in nature precursors or analogs of what later proves admirable in culture. We want to value the lush life ecosystems maintain, and the question of "helping each other out" is at most going to be a subset of this more significant issue, if "helping" is an appropriate category at all.

Painting a new picture on the conflict side, even before the rise of ecology, biologists concluded that to portray a gladiatorial survival of the fittest was a distorted account; biologists prefer a model of the better-adapted. Although conflict is part of the picture, the organism has a situated environmental fitness, including many characteristics that arc not competitive for resources or detrimental to neighbors, as when some elephants survive heat or drought better than others. The elephant fits the savannas just as much as its heart fits its liver; there is equal fittcdness within and without. There arc differences: the heart and the liver arc close-coupled; remove either and the elephant dies. Elephants and savannas are immediately weak-coupled. Elephants migrate from savannas to forests, or can be removed to zoos. But *Loxodonta africana,* removed from the selection pressures where the species evolved and its vigor is retained, soon dies too. Savannas and forests arc as necessary to elephants as hearts and livers. The more satisfactory picture is of elephants pushing to fit into a system that provides and imposes sufficient containment.

The environmental necessity involves conflict, selection pressure, niche-fittcdness, environmental support; the organic necessity involves cooperation, functional efficiency, metabolically integrated parts. The skin-in processes could never have evolved, nor can they remain what they arc, apart from the skin-out processes. Elephants are *what* they arc because they are *where* they are. What we mean by a *community* as a different systemic level from an *organism* includes these weaker, though not less valued

or fertile, couplings. The two levels are equally essential. Adaptedness covers both. This invites respect for the ecosystemic processes quite as much as organismic processes. There seems no reason to admire the inside and depreciate the outside. Else we are including only half the truth about life. In result we will mislocate our sense of duty.

Even in human society conflict is not always taken as evil. Every academic pledges to keep the critical process open, wishing the "attacks" of those who can constructively (if first destructively) spot his or her flaws. Like business, politics, and sports, ecosystems thrive on competition. In a natural community the cougars are the critics (if we may put it so) that catch the flawed deer, and thereby build better ones, as well as gain a meal Alternatively, the fleet-footed deer test out any cougars slow enough to starve. There is violence in the one process, and the other ought to be civil. Ideas die in the one realm, while individuals die in the other. Justice and charity may be relevant in culture and not in nature. But in both communities, helping is subtly entwined with competition. There is a biological, though not a cultural, sense in which deer and cougar cooperate, and the integrity, beauty, and stability of each is bound up with their coactions. Ecosystems are not of disvalue because contending forces are in dynamic process there, any more than cultures are.

Predator and prey or parasite and host require a coevolution where both flourish, since the health of the predator or parasite is locked into the continuing existence, even the welfare, of the prey and host. The one must gain maximum benefit with minimum disturbance of the other; it is to the advantage of predator and parasite to disturb prey and host species minimally. Although individuals are weakened or destroyed, if the disturbance is too great, the prey will evolve to throw off the predator, the host the parasite, or they will become rare, or extinct, to the disadvantage of predator and parasite. Parasitism tends to evolve into mutualism (e.g., cellulose-digesting bacteria in the ungulate rumen, algae and fungi synthesizing lichens, or *Chlorella* alga within the green hydra, *Hydra viridis*).

It seems doubtful that "plant defenses" are that and nothing more. Plants regulate but do not eliminate the insects that have

coevolved with them. Pollinators and fruit eaters yield benefits to and benefit from the plants they serve; insect consumers eat less than 10 percent of the terrestrial biomass upon which they graze (certain outbreaks excepted), and insects (even outbreaks of them) seem often to provide benefits of which we are as yet little aware, as we once were unaware of the benefits of fire. Aphids secrete sugars that stimulate nitrogen-fixing bacteria in the soil, and short-lived insect grazers permit to long-lived plants rapid nutrient recycling, something like that accomplished more slowly by seasonal leaf-fall and decay. Some species of grasses coevolved with grazing ungulates; neither can flourish (or even survive) without the other.[7] Here too, as with predators and prey, being eaten is not always a bad thing. Selection pressures will routinely drive adaptation and counteradaptation toward minimum disturbance, that is, to check competitions by forced cooperations.

An ecosystem is an imposing critical system, with a dialectic that keeps selection pressures high, enriches situated fitness, evolves congruent kinds in their places with sufficient containment. The ecologist finds that ecosystems objectively are satisfying environments (organismic needs are not all gratified, but enough are for species long to survive), and the critical ethicist finds (in a subjective judgment matching the objective process) such ecosystems to be imposing and satisfactory communities to which to attach duty.

It may be objected that an organism is a highly centered system; in contrast an ecosystem has no centeredness at all. The one is a marvel; the other is a muddle. The "inside" coactions routinely look teleologically constructed. Before Darwin, that fooled people into believing in design, and, whatever we think now of creation, when we come to judge the present results, humans ought to value organisms as negentropic evolutionary achievements that simulate intelligent purpose. The cooperation praised earlier can be put more precisely: *integrated cybernetic autonomy* ought to be respected.

The struggle disliked earlier can be put more simply: ecosystems are primarily *stochastic process.* A seashore, a tundra, is a loose collection of externally related parts. Even after biologists

soften conflict with adaptive fitness, a forest is mostly a game played with loaded dice. With measurable probability, red maple trees replace gray birch, and beech replace maples; each on average out-competes the other in the deepening shade. In a network of invasions there is minimal integrated process. The fox, its heart, and liver together need meat and water. But the members of a biotic community have no shared needs; there is only shoving. Or there is indifference and haphazard juxtaposition.

Much of the environment is not organic at all (rain, groundwater, rocks, nonbiotic soil particles, air). Some is dead and decaying debris (fallen trees, scat, humus). These things have no organized needs at all. The biotic sector runs by need-driven individuals interacting with other such individuals and with the abiotic and exbiotic materials and forces. Everywhere the system is full of "noise." The mathematics becomes complex; often the interactions are too messy to find regularities at all. Still, the issues are those of the distribution and abundance of organisms, how they get dispersed here and not there, birthrates and deathrates, population densities, moisture regimes, parasitism and predation, checks and balances. There is really not enough centered process to call common unity, which is why ecology has so few paradigms, and why duty directed here seems misplaced. There is only a catch-as-catch-can scrimmage for nutrients and energy.

The parts (foxes, wolves, sedges) are more complex than the wholes (forests, grasslands). Individual organisms are not decomposable; their parts (livers, hearts, culms, roots) crumple into waste outside their wholes. They cannot be divided without death, this attests to their heightened individuality.. But in an ecosystem the parts (so-called) are transients. A vixen can move her den from forest to grassland and switch prey. Migrating birds inhabit no one community but range over dozens. Ecosystems are a continuum of variation, a patchy mosaic with fuzzy edges. Some interactions are persistent, others occasional; some drive coevolution; some do not. Species in any particular ecosystem do not have the same limits to their geographical distribution; their tolerance regimes differ. There are few obligate associations. A *Juncus* species can suffer a blight and its "place" be taken by a *Carex*. An ecosystem is often transitional and unstructured;

that makes it (some say) doubtfully a natural kind at all. So far from being a satisfactory community, an ecosystem is rather sloppy.

From this perspective, the units counted as ecosystemic "parts" have more integrity than the system in which they reside. To attach duty to the loose-coupled system would misplace duty, like valuing a social institution (a business firm, a state legislature) or even a casual collection (college alumni on tour) more than the individual persons who constitute these groups. The centers of autonomy, meaningful response, satisfaction, intrinsic value, lie in the persons. However much society supplies a context of support and identity, it is *egos* that count in human ethics. By parity of reasoning, though there are no egos in nonhuman nature, we should count the nearest thing: *selves,* somatic if not psychological selves. The focal point for cultural value is the high point of individuality: the *person.* The moral focus in ecosystems should be the high point of integrated complexity: the *organism.*

This too is a picture that ecological science refocuses. Admiring concentrated unity and stumbling over environmental looseness is like valuing mountains and despising valleys. Unity is admirable in the organism, but the requisite matrix of its generation is the open, plural ecology. Internal complexity arises to deal with a complex, tricky environment. Had there been either simplicity or lock-step concentrated unity in the surroundings, no creative unity could have been composed internally. There would have been less elegance in life.

Rapid and diverse insect speciation, resulting in highly specialized forms, is a response to increasing niches in varied topographies. Complex plant biochemistries arise to produce and to offset allelopathic agents, increasing heterogeneity. The primate brain, integrated with hands and legs, is a survival tool in a "jungle." Using instinct and conditioned behavior lemurs "figure out" probabilities, there is that much order, and contingency enough to churn the evolution of skills.[8] The environment is not capricious, but neither is it regular enough to relax in. One always needs better detectors and strategies. When lions are caged, their brains degenerate within a decade; one has taken away their jungle. Simple, little-changing environments usually result in

stagnation across millennia. Dialectic with the loose environment (rich in opportunity, demanding in know-how) invites and requires creativity. The individual and the environment seem like opposites; they are really apposites; the individual is set opposed to its world but is also appropriate to it.

Further, a lack of centeredness or sharp edges does not mean a lack of relational complexity. Leopold is right to insist, against Gleason's fortuitous juxtaposition, that "the individual is a member of a community of interdependent parts" (203). Ecosystems are not as coherent as organisms, but not randomly fortuitous either; they fit together with a characteristic structure. Situated environmental fitness often yields a complicated life together. Sometimes this is in symbiosis. Spotted salamander *(Ambystoma maculatum)* eggs are invaded by a green alga that thrives on the nutrients excreted by the developing embryo, the embryo benefiting as the alga removes its wastes and provides oxygen. The tadpoles eat the algae but not before the algae produce motile cells that swim off to invade other egg masses.[9] Sometimes the interdependence is in predation. A herbivore must move to its stationary food, but that requirement alone does not yield much alertness. But since a herbivore is a food for others, and since a carnivore's food moves, the excitement increases by an order of magnitude. Sight, hearing, smelling, speed, and integrative consciousness—all of which contribute to concentrated unity—grow intense just because there is a decentralized interdependence.

The latex in milkweed is toxic to many potential grazers. Monarch caterpillars have evolved a metabolism that tolerates the latex and depend on the toxin to prevent being eaten. Blue jays eat caterpillars that graze on other plants, but not those on *Asclepais*. When caterpillars metamorphose, the toxin is concentrated in wings and legs, so that a jay that grabs a butterfly by the wings will get a bad taste and drop it. Smart jays learn to strip off the wings and legs and eat only the butterfly thoraxes. Juvenile jays do not do this instinctively and are tested for their capacity to learn it.[10] Complexity is an organism-in-environment phenomenon, from the mutations that result in *Asclepais* toxins to the demand for smarter jays. Each kind is molded by the

survival pressures of its environment; each kind has to have an adaptive fit. But each kind is creatively pushing to wedge itself in and this pushes the creativity uphill—producing smarter jays, milkweeds with novel chemistries, butterflies with novel metabolisms. And all three-milkweeds, monarch butterflies, and jays—find the system satisfactory enough to flourish in.

An ecosystem has no genome, no brain, no self-identification. It does not defend itself against injury or death as do blue jays and milkweeds. It is not irritable. An oak-hickory forest has no telos, no unified program it is set to execute. But to find such characteristics missing, and then to judge that ecosystems do not count morally, makes another category mistake. To look at one level for what is appropriate at another faults *communities* as though they ought to be organismic *individuals.* One should look for a matrix of interconnections between centers, not for a single center, for creative stimulus and open-ended potential, not for a fixed telos and executive program. Everything will be connected to many other things, sometimes by obligate association, more often by partial and pliable dependencies, and among other things there will be no significant interactions. There will be shunts and crisscrossing pathways, cybernetic subsystems and feedback loops, functions in a communal sense. One looks for selection pressures and adaptive fit, not for irritability or repair of injury; for speciation and life support, not for resisting death.

There is freedom in the interdependencies. The connections are lax; some show up only in statistics. But we do not want to see in the statistics relationships so *casual* that there is no community at all but rather relationships *causal* so as to permit genuine (loose) community, not (tight) organism. Causal links are not less significant because they are probabilistic (as one learns in physics), though they may no longer be determinate. This will be disliked by conservative ecologists and ethicists who, like Einstein, think that dice throwing is irrational. But others find that the looseness is not "noise" in the community; it is a liberal sign of beauty, integrity, and stability.

Not every collection of interacting constituents is a community. Planets form no community; plants do. The latter have an ecology, a home (*oikos*) with its logic (*logos*) of biofunctions and

resources. Molecules in a gas and moons around Jupiter have no fitness there, but caterpillars on milkweeds do. The logic of the resident home is as significant as the logic of any ephemeral inhabitant. To praise the individuals (as the creative actors) and to disparage the system (as mere stochastic, inert stage) is to misunderstand the context of creativity.

There is weak holism, not organic holism, though the weakness (if we must use that term) is a strength in the system. The looseness abets community; too much tightness would abort it. It is unlikely that there is any one defining characteristic of or correct approach to such a community. Complex and merging phenomena may be seen from numerous perspectives. Ecology may have to remain (like sociology with its several models of culture) a multiple paradigm science. Its laws will be fewer and more statistical than those in organismic biology, chemistry, or physics, because we are dealing with a community. In another sense, we do not need multiple paradigms for the community; *the paradigm is community*. Ecology discovers simultaneously (1) what is taking place in ecosystems and (2) what biotic *community* means as an organizational mode enveloping organisms. Crossing over from science to ethics, we can discover (3) the values in such a community-system and (4) our duties toward it. Interdependence does not always deliver duty, but biological obligation is a relevant consideration in determining moral obligation.

There is a kind of order that arises spontaneously and systematically when many self-concerned units jostle and seek their own programs, each doing their own thing and forced into informed interaction with other units. In culture, the logic of language or the integrated efficiency of the market are examples. No one individual orders either of these, but there is much rationality in both. In nature, an ecosystem systematically generates spontaneous order, an order that exceeds in richness, beauty, integrity, and dynamic stability the order of any of the component parts, an order that feeds (and is fed by) the richness, beauty, and integrity of these component parts. The organismic kind of creativity (regenerating a species, pushing to increase to a world-encompassing maximum) is used to produce, and is

checked by, another kind of creativity (speciating that produces new kinds, interlocking kinds with adaptive fit plus individuality and looseness).

When humans evaluate this they have a tendency to think that decentralized order is of low quality because it is uncentered and not purposive; there is no center of experience or control. We do have to be circumspect about "invisible hand" explanations, especially in culture, where there is immorality. In nature there may be clumsy, makeshift solutions. Still, everything is tested for adaptive fitness.

Regularly in ecosystems at least, such order may be a more comprehensive, complex, fertile order just because it integrates (with some looseness) the know-how of many diverse organisms and species; it is not an order built on the achievements of any one kind of thing. A culture is richer, more diverse, more beautiful because it is the product of tens of thousands of minds; it would be quite poor under the centralized control of one mind, or if all thought alike. One mind can provide or appreciate only a fraction of the wealth of a culture. Analogously, ecosystems are in some respects more to be admired than any of their component organisms, because they have generated, continue to support, and integrate tens of thousands of member organisms. The ecosystem is as wonderful as anything it contains. Producing adaptive fits and eliminating misfits, it is the satisfactory matrix, the projective source of all it contains. It takes a great world to breed great lives, great minds.

We cannot admire ecosystems until we see them as places of value capture, which is an aspect of this value integration. One can admire flight in a peregrine falcon, or the gait of a cheetah; but locomotion takes high energy funding. Muscles, nerves, and brains depend, several trophic rungs down the pyramid, on plants (99.9 percent of the biomass) that soak up the sunlight. By their concentration on capturing solar energy, stationary plants make possible the concentrated unity of the zoological world. A result is that animals, the more so the more mobile, select the communities that select them—looseness if you like, but also freedom.

Plants do not intend to help out falcons and cheetahs, nor

does any ecosystemic program direct this coaction. But the system is nevertheless a transformer that interlocks dispersed achievements. Falcons feed on warblers, which feed on insects, which feed on plants; there is a food chain from cheetah through gazelle to Bermuda grass. It is the protein in warblers which falcons can use, that in insects which warblers can use; the energy that plants have fixed is recycled by insects. The kills are the capture of skills. All these metabolisms are as linked as are liver and heart. The equilibrating system is not merely push-pull forces. It is an equilibrating of values.

The system is a game with loaded dice, but the loading is a prolife tendency, not mere stochastic process. Though there is no *Nature* in the singular, the system has a nature, a loading that pluralizes, putting *natures* into diverse kinds, $nature_1$, $nature_2$, $nature_3$, . . . $nature_n$. It does so using random elements (in both organisms and communities), but this is a secret of its fertility, producing steadily intensified interdependencies and options. An ecosystem has no head, but it has a "heading" for species diversification, support, and richness.

We do not want to extrapolate from organism to biotic community, any more than we extrapolate from culture to nature. Rather, we want criteria appropriate to this level. A monocentered organism is a tautology. A monocentered community is a contradiction in terms, though a holistic community is not. Given the logic of ecosystems, there is no reason to shut off value judgments at the skin. We want to love "the land," as Leopold terms it, "the natural processes by which the land and the living things upon it have achieved their characteristic forms (evolution) and by which they maintain their existence" (ecology) (173). The appropriate unit for moral concern is the fundamental unit of development and survival. Loving lions and hating jungles is misplaced affection. An ecologically informed society must love lions-in-jungles, organisms-in-ecosystems, or else fail in vision and courage.

On the scale of decades and centuries, ecosystems undergo succession; on the scale of centuries and millennia, they evolve. Cy-

clic systems in the short range, they are historical systems in the long range. Fires, floods, disease epidemics, windstorms. volcanic eruptions, and glaciation episodically reset succession, whether in process or at climax. One seldom travels far in a forest without evidence of fire. A majority of the resident species will find niches in the nonclimax stages. On regional scales succession is always somewhere being upset and the nonclimax species migrate accordingly. In result, all phases of succession and associated species are somewhere present. "This can seem loose and merely "fortunate." It is also a statistical "law" of ecology, an evolved characteristic of ecosystems, interruptions included, and in that sense not fortunate. As in genetics, only at a different level now, elements of randomness are incorporated in a dynamic life system. A stochastic process is loaded toward richness of life.

In succession, one species pushes out another; the competitions seem noncooperative. But there can be another way of looking at this. The pioneering species gain ground, only to make way fur later invaders that replace them. The gray birch succumb to the red maples, and beech later depend on shade provided by the maples. If, in disrupted areas (as all areas eventually are), there are no earlier species that reproduce in the sun, there can be no later species that reproduce only in shade. Waterloving plants invade the margins of a lake; as detritus collects, marsh-loving plants replace them; afterward the bog fills and broad-leaved trees can enter. On Lake Michigan shores, a sand dune starts after an unusually strong wind blowout and there· after migrates inland. Marram grass can stabilize a dune in a few years, after another decade the grass dies out; jack pine and white pine invade the dune for about a century, and after that black oak replace the pines.

"Each stage reacts upon the habitat in such a way as to produce physical conditions more or less unfavorable to its permanence, but advantageous to invaders of the next stage."[11] Species work themselves out of a home, and leave a place for what comes after. This is not always true; there are perpetually self-regenerating stands; and some species enter communities in spite of, not because of, their predecessors. But one thing that often drives suc-

cession is this remarkable competition where winners by their success alter their environment and become losers, a "fortunate" aspect of the "law" of succession, a strange environmental fitness!

Some contend that there is nothing admirable about succession or its periodic upset, nor about beech depending on the maples whose ground they invade. Yet after one has become ecologically sensitive, the system is a kaleidoscope, it turns round with the accidental tumbling of bits and pieces, each with its own flash and color, and yet the whole pattern is also of interdependent parts coacting, patterns repeated over time and topography, endlessly variable, and yet regular, buzzing with life.

And there is much more. Succession is a subroutine in a dramatic story.

It is sometimes said that ecosystems are Markov processes, that is, stochastic systems without long-term memory.[12] The succession from state A (subclimax) to state B (climax) can be specified without attention to history. Whether dice thrown today will come up deuce is independent of what the throws last month were. Whether the maples push out the birch on the east side of the Wisconsin River in the next decade is independent of whether they did this on the west side in the last decade. By contrast, higher organisms and especially persons in cultures are historical entities. Whether the coyote falls for the trap depends on its earlier experiences. Whether a nation passes from state A (peace) to state B (war) depends on lessons learned in the past. As a person matures, the quality of life depends upon cumulative reaction patterns. Ecosystems have no analogous "character." Unlike coyotes or blue jays, they learn nothing. They simply undergo succession, episodically reset. This can seem to give ecosystems less identity and worth in contrast to persons and intelligent organisms. Noncognitive systems deserve little respect, none at all if clumsy and inelegant.

But over evolutionary time ecosystems are quite historical, although decentralized. There is an enormous amount of history in a handful of humus, contrasted with a handful of lunar soil, in the sense that what goes on there bears the memory (cognitive information coded in DNA) of discoveries in previous millennia of Earth's history. This makes biology different from chemistry.

One extrapolates mineralogy on Earth to Jupiter and Mars, but one extrapolates nothing extraterrestrially from the birch-maple-beech succession, because earthbound successions are historically evolved phenomena. The birch have "memories," "experiences," strategies accumulated over tens of thousands of years. Black walnuts and *Salvia* shrubs "remember" how to inhibit their competitors. Some of the biochemistries (like photosynthesis) are a billion years old. The behavior of the marmot, hibernating at the onset of winter, is not a probabilistic reaction to cold, but a historically conditioned instinct. An ecosystem has "heritage," a "tradition," the principal cause of what is taking place.

Yet there are surprises. No ecologist can predict successions a thousand years hence, nor are paleobiogeographers surprised when pollen analysis reveals that they were something else a thousand years ago. New historical developments take place.[13] Ecosystems have weak laws and few "constants," only statistical mathematics, no comprehensive theories, all of which can dismay a scientist anxious about predictions. But this can delight the philosopher who finds the laws sufficient constantly to generate history and who finds historical communities satisfying. This liberal environment proves both empirically necessary and sufficient (requisite and satisfying) for producing life, and yet fails to be logically necessary and sufficient (yielding hard deterministic laws). Yet a closed necessary and sufficient environment (a deterministic one) would logically and empirically prevent both the historicity and the individuality we admire within ecosystems. It would block potential and openness. The ecosystem is contingently sufficient for what takes place in it. The ethicist finds this satisfying, contingently sufficient for generating duty.

The species of the community are something like the genes of an organism (said A. G. Tansley).[14] Despite differences between organisms and communities, the analogy correctly teaches that, just as the organism is not its genes but has its history stored there, the community history is not merely that of its species, although the history is written there. The context of history is not all privately in individuals, though the sectors relevant to particular individuals are coded in their DNA strands. History is

smeared out across the system. Some is concentrated in the DNA sequences of the birch tree, some in the individual coyote's career, and that diffused in the biotic community as a matrix of coevolved historical centers is equally remarkable. All the transmissible memory is somewhere in the genetic pool, but to think that history is all pinpointed in individuals because the DNA that stores it is within organisms would be as mistaken as to think that human history was all in the books that record it. The impetus for history is as much in the system-place as in the member inhabitants.

A technical way of summarizing this is that communities, not less than individuals, are as idiographic as they are nomothetic.

Perhaps the good of the community, spoken of collectively, is just the goods of individuals distributively, conveniently aggregated rather like a center of gravity in physics focuses at a point the masses of myriads of particles. Is the "community" a meta·phor for the goods of individuals, not something else from it, rather similar to the way in which the goods of United States citizens are summed up as "the nation"? When a hiker has seen all the trees, and asks next, "show me the forest," he has not understood that the forest is nothing more than the trees. Some community-level epiphenomena appear—communities have trophic patterns and organisms do not—but the phenomena are merely interacting individuals. There is complicated life together, but without emergent system-level properties. The system is an ontological fiction. On the other hand, all nominalists soon learn to fear a slippery slope: communities are fictions, their organisms are real; organisms are fictions, their organs are real; organs are fictions, their cells are real; and so on down to quarks.

After one has discarded category mistakes and associated prejudices for skin-in cooperation, centeredness, and so forth, there seems little reason to count one pattern (the organism) as real and another (the ecosystem) as unreal. Any level is real if there is significant downward causation. Thus the atom is real because that pattern shapes the behavior of electrons; the cell because that pattern shapes the behavior of amino acids; the orga-

nism because that pattern coordinates the behavior of hearts and lungs; the community because the niche shapes the morphology and behavior of the foxes within it. Being real at the level of community does not require sharp edges, or complex centeredness, much less permanence, only organization that shapes, perhaps freely so, the behavior of member/parts.

Humans may not have duties at every such level of organization. But humans have duties at appropriate survival-unit levels. The organism is one kind of survival unit, as the liver is not. The ecosystem is another critical survival unit, without which organisms cannot survive. The patterns (energy flow, nutrient cycles, succession, historical trends) to which an organism must "tune in" are set "upstairs," though there are feedback and feedforward loops, and system-level patterns are altered by creativity in individual-level mutations and innovations. Editing and support come "from outside" the boundary, "from above" the level of the organism. The community forces are prolific, though they also are stressful forces from the perspective of the individual.

. Has the community priority over the individual? Individuals are ephemeral and dispensable, role players in a historical drama where even ecosystems—indispensable and perennial in native-range time frames—enter and exit on geological time scales. The prescription that seems to follow such a description is that communities dominate individuals, since that is the (supposedly admirable) way that nature operates. But moving from *is* to *ought* this way counters the respect for individual autonomy that has become the trademark of liberalism. Community dominance becomes a totalitarian juggernaut. Ethicists would at once censure a social community crushing individuals. Ethics has fought to protect individuals from the tyrannies of culture. Must environmental ethicists reverse hard-won victories and give the community priority? So to trump the individual seems retrogressive.

This fear is a confusion. Had Leopold said, "A thing is right when it tends to preserve the integrity of the human *social* community," he would have on his hands most of the arguments between utilitarian and rights theorists, as well as disputes between liberal and conservative social theorists. A considerable case can be made for the descriptive fact that social forces do shape per-

sons, they induce behavior more than liberals like to admit, and a less considerable case can be made that this ought to be so. Individuals who test whether personal preferences are right by asking what they do to the good of nation, church, or heritage do not always have their priorities reversed. Leopold does think that ethics "tries to integrate the individual to society" and limits freedom in order to favor cooperative social conduct (203). Any social contract theorist would endorse as much.

But Leopold is making no serious claims about interhuman ethics. Nothing really follows from what *is* or *ought to be* in culture to what *is* or *ought to be* in nature. Sociologists, their studies of society in hand, would not tell ecologists what they must find descriptively about ecosystems; that would be a category mistake. Cultures are a radically different organizational mode. Social philosophers, with justice and charity praised in moral society, cannot tell environmental ethicists what is right and wrong in amoral ecosystems, nor what is so when humans deal with ecosystems, radically different from culture.

As humans gain a description of how ecosystems work, Leopold believes that a prescription arises to respect the beauty, integrity, and stability of such systems. That is not all of ethics, only an extension of it. Duties to other humans remain all they have ever been, but "the land" now counts too. Duties to humans (feeding the starving) in conflict with duties to ecosystems (preserving tropical forests) remains a quite unfinished agenda, but Leopold only wanted to start a dialogue that could not begin when the land had no "biotic right" at all (211).

Relations between individual and community have to be analyzed separately in the two communities. To know what a bee is in a beehive is to know what a good (functional) bee is in bee society, but (*pace* sociobiologists) nothing follows about how citizens function in nation-states or how they ought to. And vice versa. So, when humans confront beehives, complaints about a totalitarian society are confusions. Likewise, whether there are duties to ecosystems must be asked without bias from human society. It may be proper to let Montana deer starve during a rough winter, following a bonanza summer when the population has edged over the carrying capacity. It would be monstrous to be so

callous about African peoples caught in a drought. Even if their problems are ecologically aggravated, there are cultural dimensions and duties in any solution that are not considerations in deer management.

In biotic communities, the community is the relevant survival unit; its beauty, integrity, and stability come first. Feral goats on San Clemente Island are degrading the ecosystem and authorities are eliminating the goats, overriding individual goat welfare out of respect for the ecosystem. In Yellowstone National Park, when an outbreak of pinkeye threatened the bighorn sheep, park officials refused to treat the disease, although half the herd was blinded and died through starvation and injury. Their argument was that the Yellowstone ecosystem should be preserved as untampered as possible, and that these processes included the struggle between mammals and their natural parasites. Foresters may let wildfires burn, destroying individual plants and animals, because fires rejuvenate the system.

But we need to bring back into focus the looseness, decentralization, and pluralism of biotic communities. Individual organisms are so tightly integrated that we do not term them *communities* at all. No one complains that the goods of heart and liver are only instrumental to the good of the organism. But communities, social or biotic, never have this kind of organization. Biotic communities leave individuals "on their own," autonomous centers, somatic selves defending their life program. (Consistently with this, Yellowstone bighorns should be left "on their own" to combat the *Chlamydia* microbe.

Ecosystems bind life up into discrete individuals and cast them forth to make a way resourcefully through their environment. So far from being a regimented community, the wilderness has seemed anarchy to many observers, who are more likely to complain of the pulling and hauling that there is no community at all, than to complain that the individual is subordinated to the community. The picture we need, however, is of community that packages everything up into individual lives and binds them together loosely (that is, freely) enough that individuals remain gems in a setting, yet tightly enough that the generating, maintaining system is prior to individual life.

Evolutionary ecosystems maximize individuality in several ways. First, the stochastic contingencies and idiographic historicity that beset every particular organism differentiate their characteristics and fortunes. There is a wildness in ecosystems that resists being completely specified in geology, botany, zoology, and ecology textbooks, even when principles set forth there are coupled with initial conditions. Scientific laws never catch in individual detail all that goes on in a particular place, such as Okefenokee Swamp or Bryce Canyon. Each new lake and canyon will have some differences. No matter how well one knows a particular place, tomorrow and next year will bring surprises.

This is logically and empirically entwined with the heightened individuality of each inhabitant. Each life is given a unique genetic set and lived in a unique place. Some unrelated causal lines and even indeterminate lines meet and make every individual a one-time event. No two coyotes in Bryce Canyon or even two cypress trees in Okefenokee Swamp are alike. Sometimes the differences are insignificant, but sometimes they yield significant individuality. Any organization that removed the diversity, the looseness, the "disorder," the historical particularity of place and individual, would impoverish the ecosystem and the individuality of its member individuals.

Second, evolutionary ecosystems over geological time have steadily increased the numbers of species on Earth from zero to five million or more. Extinction and respeciation have increasingly differentiated natural kinds. Leopold wrote, "Science has given us many doubts, but it has given us at least one certainty: the trend of evolution is to elaborate and diversify the biota" (216). R. H. Whittaker found that on continental scales and for most groups "increase of species diversity. . . . is a self-augmenting evolutionary process without any evident limit." There is a tendency toward "species packing."[15] G. G. Simpson concluded that there is in evolution "a tendency for life to expand, to fill in all available spaces in the livable environments, including those created by the process of that expansion itself. . . . The total number and variety of organisms existing in the world has shown a tendency to increase markedly during the history of life."[16] Islands, though limited in their capacity to carry species,

produce isolated kinds. Nature seems to produce as many species as it can; although locally poor in a desert or on a polar ice cap, in the aggregate Earth's ecosystems are many-splendored things. Charles Elton found that five thousand species of animals inhabited two square miles of Wytham Wood in Britain.[17]

Third, superimposed on this increase of quantity, the quality of individual lives in the upper trophic rungs of the ecological pyramid has risen. One-celled organisms evolved into many-celled, highly integrated organisms. Photosynthesis supports locomotion—swimming, walking, running, flight. Stimulus-response mechanisms become complex instinctive acts. Warm-blooded animals follow cold-blooded ones. Neural complexity, conditioned behavior, and learning emerge. Sentience appears—sight, smell, hearing, taste, pleasure, pain. Brains couple with hands. Consciousness and self-consciousness arises. Persons appear with intense concentrated unity, and nature transcends itself in culture. These are liberating developments in the ecosystem; they free individuals. A falcon is more liberated in its ecosystem than is the grass downward in its food chain; it can overlook a territory, migrate, switch prey. This is community looseness now interpreted positively as nourishing individuality.

These developments do not take place in all ecosystems nor at every level. Microbes continue, as do plants and lower animals. These kinds serve continuing roles. All the understories remain occupied. If they did not, the quantity of life and its diverse qualities would diminish. Most creatures are cryptogams, dicots, monocots, fungi, bacteria, protozoans, beetles, mollusks, crustaceans, and the like. Sometimes, there is retrograde evolution, as in tapeworms or viruses, when once free-living organisms lose eyes, legs, metabolisms, or even brains, although retrograde evolution requires that such organisms live in an environment more complex than they are themselves, so that they can borrow their lost skills from their hosts. Meanwhile, the quality of individuality generated at the top rises. So both the quantity and the quality of individuality intensify. This continues despite at least five catastrophic extinctions, so anomalous that many scientists look to extraterrestrial causes: supernovae, collisions with asteroids or oscillations of the solar system above and below the plane

of the galaxy. Regardless of their causes, the crashes are followed by swift resurrections, often with novel and advanced forms. Optimization of fitness seems to increase through evolutionary time.[18] There are vastly more individuals and species and they are better fits in their communities.

These developments in natural history are not just a random walk, not just drift. They reveal the rationality of the system, including trial and error. Spasmodic on short ranges, rather like the episodic upset of succession, these prolific trends are a recurrent tendency on long-range scales. Sometimes the evolutionary (as do the ecosystemic) processes seem wandering and wayward, loose, but the results are considerable. There is dice-throwing, but the dice are loaded. The probabilities are showing causal connections, laws.

The community beauty, integrity, and constancy include selecting for individuality. That is a strange, liberating "priority" or "heading" of the system: escalation of individuals in kind and complexity, in quantity and quality, never producing two of a kind exactly alike! That process is as much to be defended as any of its products. The goods and "rights" of individuals (their flourishing and freedom) belong in such a system; the ecosystem itself promotes them in its own way. When humans enter the scene, they should in this respect follow nature. Individual welfare is both promoted by and subordinated to the generating communal forces.

Instrumental value uses something as a means to an end, intrinsic value is value as an end in itself without necessary contributory reference. Leopold laments that nature has previously been considered to have only instrumental value for humans, regarded as the sole holders of intrinsic value. Those sensitive to ecology will revise their axiology. An immediate conclusion is that, apart from any human presence, organisms value other organisms and earth resources instrumentally. Organisms are selective systems. Plants make resourceful use of water and sunshine. Insects value energy fixed by photosynthesis; warblers value insect protein; falcons value warblers. Value capture propels an ecosystem. An organism is an aggrandizing unit on the hunt for instrumental values.

Continuing this logic, organisms value these resources instrumentally because they value something intrinsically: their selves, their form of life. No warbler eats insects in order to become food for a falcon; the warbler defends its own life as an end in itself and makes more warblers as she can. A life is defended intrinsically, without further contributory reference—unless to defend the species and that still is to defend a form of life as an end in itself. Such defenses go on before humans are present; and thus both instrumental and intrinsic values are objectively present in ecosystems. The system is a web where loci of intrinsic value are meshed in a network of instrumental value.

Neither of these traditional terms is completely satisfactory at the level of the holistic ecosystem. Member components serve roles, as when warblers regulate insect populations; perhaps that is systemic instrumental value. But, reconsidering, the decentered system, despite its successions and headings, has no integrated program, nothing it is defending, and to say that an ecosystem makes instrumental use of warblers to regulate insect populations seems awkward. We might say that the system itself has intrinsic value; it is, after all, the womb of life. Yet again, the "loose" system, though it has value in itself, does not seem to have any value for itself, as organisms do seem to have.

Nevertheless the system has these characteristics as vital for life as any property contained within particular organisms. Organisms defend only their own selves or kinds, but the system spins a bigger story. Organisms defend their continuing survival; ecosystems promote new arrivals. *Ecosystems are selective systems, as surely as organisms are selective systems.* This extends natural selection theory beyond the merely tautological formulation that the system selects the best adapted to survive. The system selects for what appears over the long ranges, for individuality, for diversification, for sufficient containment, for quantity and quality of life. Appropriately to the community level, ecosystems select employing conflict, decenteredness, probability, succession, and historicity.

We are not any longer confronting instrumental value, as though the system were of value instrumentally as a fountain of life. Nor is the question one of intrinsic value, as though the system defended some unified form of life for itself. We have

reached something for which we need a third term: systemic value. This cardinal value, like the history, is not all encapsulated in individuals; it too is smeared out into the system. The value in this system is not just the sum of the part-values. Systemic value is the productive process; its products are intrinsic values woven into instrumental relationships. When humans awaken to their presence in such a biosphere, finding themselves products of this process too—whatever they make of their cultures and anthropocentric preferences, of their duties to other humans or to individual animals and plants—they owe something to this beauty, integrity, and constancy in the biotic community. Ethics is not complete until extended to the land.

Some will object: cooperation versus conflict, centered cybernetic autonomy versus loose stochastic process, succession and natural history, systemic values—none of this has touched the nerve of the matter. The final, fundamental problem is that ecosystems have no subjectivity, no felt experiences. Organisms with central nervous systems have psychological life, manifestly present by introspection in human lives, and easy to extend to some nonhumans—more so to chimpanzees, less so to birds. Plants are objects with life, but not subjects of a life. But ecosystems are doubtfully objects at all, rather they are communities mostly of living objects and sparsely of living subjects. No such collection can of itself count morally; any duties must attach to the few subjects who inhabit such places.

An ecosystem cannot be satisfied when given wilderness status; a person can be satisfied when a wilderness is designated. Even coyotes can be satisfied within such a wilderness. Such psychological satisfaction is what the inside/outside issue should have been identifying. The skin is not a morally relevant boundary; rather the boundary is subjective inwardness versus objective metabolisms and ecologies. Duties may *concern* ecosystems but must be to subjects.

The attractiveness of the duties-to-subjects-only position is that the duties we first know in interhuman ethics are to subjects, and an ethicist can always stipulate that duties stay directed toward subjects. A mere object, even one with life, is a misplaced

target for duty. This can seem right because it is so familiar. Any duties that involve living or nonliving objects must be reduced to duties to subjects. No doubt some duties do attach only to subjects; some make sense only with human subjects. Persons ought not to be insulted, but squirrels do not suffer much from verbal insults. One may have duties to subjects of a psychological life not to cause needless pain, perhaps not to interfere with their pleasures without justification. We have duties to persons to preserve the integrity, beauty, and stability in the biotic communities that these persons enjoy and resourcefully use. Leopold would endorse such duties, but they are not the only kind he is proposing.

From the ecological point of view the subjectivist position takes a part for the whole. It has a subjective bias. It values a late product of the system, psychological life, and subordinates everything else to this. It mistakes a fruit for the whole plant, the last chapter for the whole story. It orders all duty around an extended pleasure-pain axis, richer through poorer experiences. Such an ethic is really a kind of psychological hedonism, often quite enlightened. But ecosystems are not merely affairs of psychological pains and pleasures. They are life, flourishing in interdependencies pressed for creative evolution. The satisfaction defended at this level is not subjective preferences but the sufficient containment of species.

Leopold does not want a subjective morality but an objective one. He presses this question: Is there any reason for ethical subjects to discount the vital systemic processes unless and until accompanied by sentience? Perhaps to evaluate the entire biological world on the basis of sentience is as much a category mistake as to judge it according to justice and charity found there. The one mistake judges biological places by extension from psychology, the other from culture. What is "right" about the biological world is not just the production of pleasures and positive experiences. What is "right" includes ecosystemic patterns, organisms in their generating, sustaining environments.

True, the highest value attained in the system is lofty individuality with its subjectivity, present in vertebrates, mammals, primates, preeminently in persons. But such products are not the

sole loci of value, concentrate value though they may. The objective, systemic process is an overriding value, not because it is indifferent to individuals, but because the process is both prior to and productive of individuality. Subjects count, but they do not count so much that they can degrade or shut down the system, though they count enough to have the right to flourish within the system. Subjective self-satisfactions are, and ought to be, sufficiently contained within the objectively satisfactory system. The system creates life, selects for adaptive fit, constructs increasingly richer life in quantity and quality, supports myriads of species, escalates individuality, autonomy, and even subjectivity, within the limits of decentralized community. If such land is not an admirable, satisfactory, morally considerable biotic community—why not?

Notes

The author gratefully acknowledges critical help from Andrew Brennan and Bruce Omundson.

1. F. E. Clements, *Research Methods in Ecology* (Lincoln,Neb.: University Publishing Co., 1905, 199..

2. H. A. Gleason, "Delving into the History of American Ecology," *Bulletin of the Ecological Society of America* 56. no. 4 (December 1975):7-10, citation on 10.

3. See an early essay, not published during Leopold's life," Some Fundamentals of Conservation in the Southwest," *Environmental Ethics* 1 (1979):131-141. Leopold has abandoned all but the echoes of any philosophy of organism in *A Sand County Almanac*. See J. Baird Callicott, "'The Conceptual Foundations of the Land Ethic" (in this volume) for a thorough discussion.

4. See J. Baird Callicott, "Hume's Is/Ought Dichotomy and the Relation of Ecology to Leopold's Land Ethic," *Environmental Ethics 4* (1982): 163-74.

5. The best discussion of conceptual issues in ecology is Esa Saarinen, ed., *Conceptual Issues in Ecology*,parts 1 and 2, *Synthese* 43, nos. 1 and 2 (January and February 1980). This collection is largely reprinted as Esa

Saarinen, *Conceptual Issues in Ecology* (Dordrccht, Holland: D. Reidel Publishing Co., 1982). For another discussion of "how to think about ecosystems, and how to place them within the scheme of known systems," see J. Engelberg and L. L. Boyarsky, "The Noncybernetic Nature of Ecosystems," *American Naturalist 114(1979):317-24,* citation on 3l3, and in rebuttal Bernard C. Patten and Eugene P. Odum, "The Cybernetic Nature of Ecosystems," *American Naturalist* 118(1981):886-95.

6. John Passmore, *Man's Responsibility for Nature* (New York: Charles Scribner's Sons, 1974), 116.

7. D. F. Owen and R. G. Wiegert, "Do Consumers Maximize Plant Fitness?" *Oikos* 27(1976):488-92; D. F. Owen, "How Plants May Benefit from the Animals that Eat Them," *Oikos* 35(1980):230-35. D. F. Owen and R. G. Wiegert, "Mutualism Between Grasses and Grazers: An Evolutionary Hypothesis," *Oikos* 36(1981)376-78, and a subsequent discussion in *Oikos* 38(1982):253-59; W. J. Mattson and N. D. Addy, "Phytophagous Insects as Regulators of Forest Primary Production," *Science 190(1975):515-22; S.* J. McNaughton, "Serengeti Migratory Wildebeest: Facilitation of Energy Flow by Grazing," *Science* 191 (1976):92-94; S. J. McNaughton, "Grazing as an Optimization Process: Grass-Ungulate Relationships in the Serengeti," *American Naturalist* 113(1979)691-703.

8. This point is elaborated by Paul Shepard, *Thinking Animals* (New York: Viking Press, 1978).

9. P. W. Gilbert, "Observations on the Eggs of *Ambystoma maculatum* with Especial Reference to the Green Algae Found Within the Egg Envelopes," *Ecology* 23(1942)215-27, and further comment 25 (1944): 366-69.

10. L. P. Brower and S. C. Glazier, "Localization of Heart Poisons in the Monarch Butterfly," *Science* 188(1975):19-25.

11. Clements, *Research Methods in Ecology*, 265. An analogue of this in evolutionary development is the tendency of winners to overspecialize and to become extinct in changing environments, losing out to the less specialized.

12. Henry S. Horn, "Markovian Properties of Forest Succession," in *Ecology and Evolution of Communities*, ed. Martin L. Cody and Jared M. Diamond (Cambridge: Harvard University Press 1975), 196-211.

13. H. E. Wright, Jr., "The Roles of Pine and Spruce in the Forest History of Minnesota and Adjacent Areas," *Ecology* 49(968):937-55.

14. A. G. Tansley, "The Use and Abuse of Vegetational Concepts and Terms," *Ecology* 16(1935):284-307, citation on p. 290.

15. R. H. Whittaker, "Evolution and Measurement of Species Diversity," *Taxon* 21(1972):213-51, citation on 214.

16. G. G. Simpson, *The Meaning of Evolution* (New Haven: Yale University Press, 1964), 243, 341.

17. C. S. Elton, The Pattern of Animal Communities (London: Methuen and Co., 1966), 62.

18. D. M. Raup and J. J. Sepkoski, Jr., "Mass Extinctions in the Marine Fossil Record," *Science* 215(1982):1501-3.