Terrestrial Habitats of Southeast Alaska

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Introduction

Southeast has a wide variety of terrestrial habitats. In this rainy region, where waterlogged soils prevail, soil drainage is a key determinant of habitat type. Among terrestrial habitats, well-drained surfaces typically support forest, while poorly drained surfaces support non-forested or sparsely forested wetlands.

In addition to drainage, other primary influences on terrestrial habitat diversity include successional age–or time since last substantial vegetation disturbance–and elevation above sea level. Collectively, these 3 primary factors exert control over habitat character throughout Southeast and their influence can be clearly seen on virtually every site. Secondary influences, such as aspect, climate, bedrock geology, and other living things (biotic influences) are locally important but most evident in more extreme situations. In bioregions outside of Southeastern Alaska, such influences are often considered equal in importance to the 3 factors identified here as primary influences.

PRIMARY INFLUENCES

Drainage

On most lowland, well-drained sites, succession eventually leads to forest (at higher elevations well-drained sites support alpine tundra). On wet and poorly drained sites, woody-stemmed plants may only occur on elevated microsites (Fig 3).
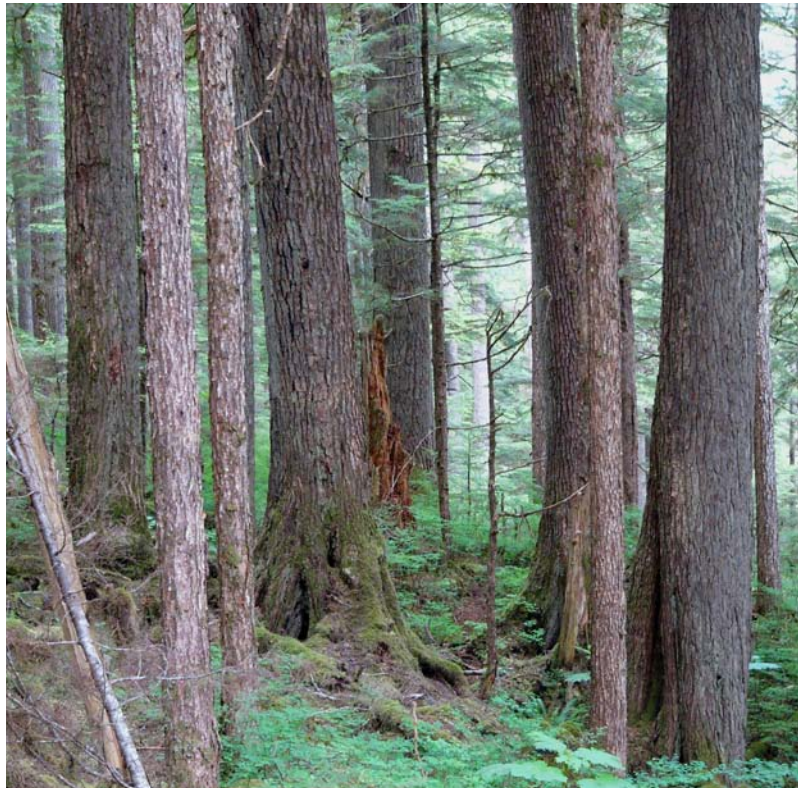
FIG 1. Western hemlocks, Tuxekan Island.

In intermediate drainage situations it can be difficult to draw clear lines between habitat types. Scrubby old-growth forest, for example, is usually stunted because of poor drainage. Small-tree stands may be classified as forested wetland in the National Wetlands Inventory (NWI) database, but still get include in the Productive Old Growth (POG) classification in the USFS timber database as long as their estimated wood volume is greater than 8,000 net board feet per acre (.4 ha).

Age

Within each of the 2 drainage categories, habitats may be further subdivided according to plant successional status. The course of succession is determined in part by the character of the last major site disturbance. Post-glacial forest development, for example (primary succession), is very different from post-logging development (secondary succession).

Elevation

Changes to habitat with elevation are poorly documented in Southeast. But if anything, the mosaic of community types near tree line is more complex and variable than at sea level. Following descriptions of forest and early successional types, the subalpine forest, subalpine parkland, and alpine elevational zones are discussed.

Of these 3 primary influences on habitat type– drainage, age, and elevation–the first and last are fairly well mapped throughout Southeast. Age or successional stage, however, is more difficult to interpret from remote sensing, and is labor-intensive to measure on the ground. Only logged second-growth from the past half century is shown on Tongass-wide maps (the "managed stands" data layer); other types of early successional habitats remain unmapped.

SECONDARY INFLUENCES

Aspect

Aspect or slope direction, controls forest habitat in Southeast in several ways; however, they are somewhat indirect and rather inconsistently expressed. Unlike in drier bioregions where striking north-south habitat variation stems from differences in sun exposure and soil moisture, the Southeast aspect differences are more strongly keyed to wind. Slopes facing into the prevailing southerly storm winds are more exposed to occasional blowdown events that lead to replaced forest stands. Therefore, south-facing exposed slopes tend to have younger, more even-aged stands, and north-facing lee slopes tend to have older, uneven-aged stands (Nowacki and Kramer 1998).

In areas with heavy deer populations, steep south-facing forested slopes have less snow and attract more deer use in winter. High concentrations of deer

may result in a more open understory, with forage shrubs browsed down below knee height, whereas north-facing slopes retain thicker brush (Schoen and Kirchhoff 1990).

Climate

In general, the annual temperature and precipitation regime does not vary enough at a given elevation within most of Southeast to account for obvious differences in habitat. Exceptions include the transboundary river bottoms and the extreme outer coast (Fig 2).

Bedrock Geology

The influence of *surficial* geology on habitat is expressed largely through substrate permeability; however, bedrock type ("parent material") also exerts chemical influences. For example, acid-buffered limestone and marble bedrock can result in exceptionally productive communities.

Biotic influences

Certain animal species, like beaver (*Castor canadensis*)—termed a keystone species—are so influential that they alter the structure and composition of the plant community. Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), for example, are nearly ubiquitous on the islands and mainland of Southeast. But their population density varies with factors such as snow depth and wolf predation. Where overwintering deer are most

FIG 2. View up the Meade Glacier into British Columbia. Headwaters of the Katzehin River near Haines, this transboundary watershed spans a huge climatic gradient from dry, boreal interior to wet coastal rain forest.

LOWLAND TERRESTRIAL HABITATS OF SOUTHEAST ALASKA
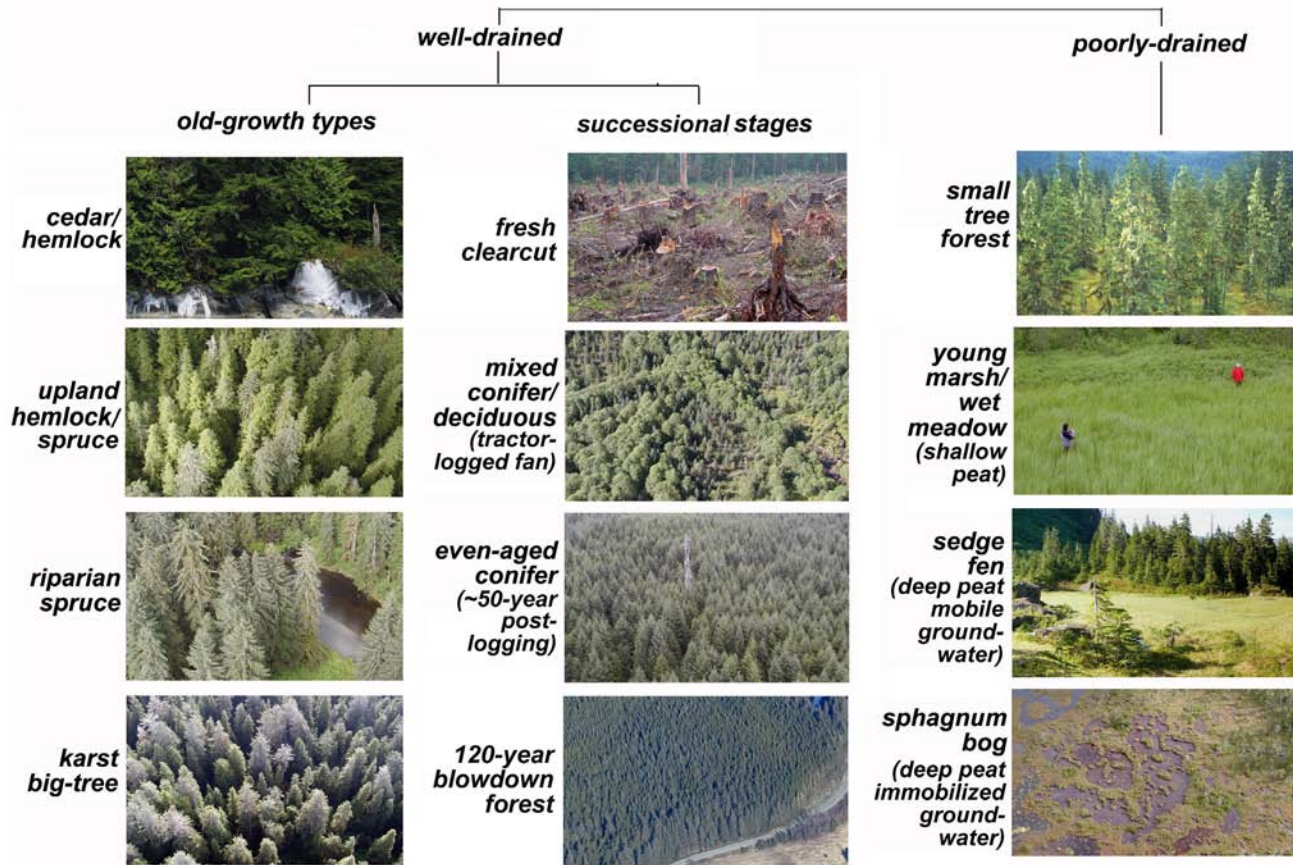
FIG 3. Flowchart illustrating 2 of the 3 primary influences on this report's habitat classification, with emphasis on habitats of conservation concern. Habitats are first divided into well- and poorly drained groups. Well-drained habitats eventually support old-growth forest types (left column) that vary mostly according to substrate character. This forest sequence represents increasingly productive and better drained sites from cedar forests to karst big-tree forest. The center column follows a successional series from early post-logging to even-aged conifer habitats. The last, right-hand column representing poorly-drained habitats begins with small-tree forests on soils too wet for optimal tree growth. Among non-forested wetland types, younger marshes or wet meadows (shallow peat) can be distinguished from ancient, deep-peat habitats called bogs and fens depending on the movement of ground water.
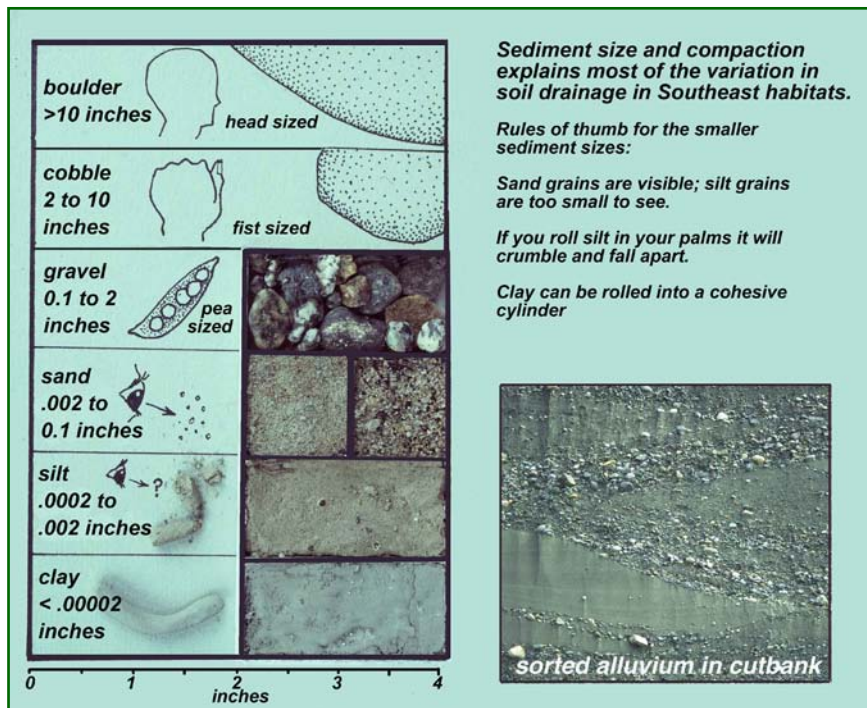
FIG 4 . Sediment size is the primary determinant of soil drainage. Each landforming agent leaves distinctive sediment types.

FIG 5. Wide range of old-growth structure east of Big Salt Lake, Prince of Wales Island. Scrub forest in lower left may be as old as the tall spruces in upper right. The primary influence on forest variation in this scene is soil drainage.

abundant, as on low-snow, wolf-free, outer Yakobi Island, most woody browse species are greatly reduced in abundance, resulting in park-like forest understories. Nearby, on the mainland north of Cross Sound, deer are absent and blueberry (*Vaccinium* spp.) thickets can be so dense that hiking is a challenge.

HABITAT CLASSIFICATION SYSTEMS

There are several parallel classification systems for Southeast terrestrial habitats. In Table 1 these classifications are compared. The units in column A are the most conceptually encompassing. They combine topographic and elevational position with canopy closure and broad species groupings to describe essentially all of the forest types in Southeast. Column B, in contrast, prioritizes forest types of conservation concern detailed in this report. In some cases–such as karst large-tree forest–the units are more restrictive than those of pre-existing classifications. In other cases–such as wet, small-tree forest–the units are broader, embracing more than a dozen of the units based on species composition. Column D lists the USFS Region 10 plant series (DeMeo et al. 1992) that are founded on dominant tree species.

Yet another forest-type system is the structurally-based classification that employs mean tree size and stand density (Caouette and DeGaynor 2005). This system is described in a sidebar below (Mapping Forest Structure). The value of the size/density model is that, unlike classifications based on species composition, these units can be mapped to a degree of accuracy acceptable for some management and interpretive purposes. They also effectively characterize forest types with distinctive ecologic and economic value.

The Caouette structural (size/density) classification cannot effectively be "crosswalked" with columns A or D in Table 1 that are founded primarily upon species composition. These latter compositional types describe "potential" vegetation; that is, they can include any successional stage from saplings to old growth, thus encompassing many different size/density classes. Column B, however, does permit some correlations with the size/density classification, because in some cases it is more specific about stand structure and age. These correlations are shown in Table 2.

In the following sections, habitats generally have been named and defined to correspond with existing geographic information system (GIS) data layers consolidated for this project by The Nature Conservancy and Audubon Alaska primarily from resource agencies, including the USFS, FWS, ADF&G. With some exceptions, the habitats described below can be mapped region-wide by using combinations of these GIS data layers.

TABLE 1. The habitat classification system used in this report focuses on forest types of special conservation concern.

Comparison of various compositional and structural classifications of major Southeast forest-types [1]

Topographic/compositional units [2] A	Units of conservation concern described in this report [3] B	Dominant species C	R-10 plant associations [4] D
Closed-canopy forests (well-drained) [5]			
riparian spruce-hemlock forest	riparian large-tree spruce, young even-aged conifer	*Picea sitchensis*	sitka spruce series
upland hemlock-spruce forest	upland hemlock/spruce, karst large-tree young even-aged conifer	*Tsuga heterophylla-Picea sitchensis*	western hemlock series(5)
upland hemlock-cedar forest	cedar/hemlock, wet, small-tree, young even-aged conifer	*Tsuga heterophylla-Thuja plicata*	western hemlock-redcedar series(7)
upland hemlock-cedar forest	cedar/hemlock, wet, small-tree, young even-aged conifer	*Tsuga heterophylla-Chamaecyparis nootkatensis*	western hemlock-yellowcedar series
lowland mixed conifer forest	upland hemlock/spruce, wet, small-tree, young even-aged conifer	*Tsuga heterophylla-Tsuga mertensiana-Pinus contorta*	mixed conifer series(8)
lowland mixed conifer forest	wet, small-tree	*Pinus contorta-Tsuga heterophylla-T. mertensiana*	shore pine series(4)
subalpine mixed conifer	subalpine forest subzone	*Tsuga heterophylla-Tsuga mertensiana-Picea sitchensis*	mountain hemlock series
Open-canopy forests (poorly drained) low elevation [6]			
mixed conifer woodland [7]	wet, small-tree	*Pinus contorta-Tsuga heterophylla-T. mertensiana*	shore pine series(4)
mixed conifer woodland	wet, small-tree	*Tsuga heterophylla-T. mertensiana-Pinus contorta*	mixed conifer series(8)
mixed conifer woodland	wet, small-tree	*Tsuga heterophylla-Thuja plicata*	western hemlock-redcedar series(7)
Open-canopy forests (mostly well drained), high elevation			
subalpine woodland	subalpine parkland subzone	*Tsuga mertensiana*	mountain hemlock series
subalpine mixed conifer	subalpine forest	*Picea sitchensis-Tsuga mertensiana*	high elevation Sitka spruce series [8]

1 The size/density-based structural classification (Caouette and DeGaynor 2005) effectively captures units of distinct ecologic/economic value, and can be depicted on forest-type maps. However these units (SD-67, SD-4H, etc) cannot be directly correlated with units based primarily on species composition.

2 These units combine topographic and elevational position with canopy closure and broad species groupings to encompass all Southeast forest types.

3 Units of conservation concern described in this report are in some cases more specific than existing classifications. In other cases - e.g. wet, small-tree forest - they are broader, more inclusive units. Primary criteria are: 1) high ecologic/economic value; 2)"mappability;" 3) age/structural specificity for key types.

4 Units of the R10 classification (DeMeo et al. 1992). These units are ecologically significant but cannot currently be mapped from remote sensing. Number in parenthesis refers to the number of plant associations (habitat types)

5 According to Viereck et al. (1992) closed canopy is defined as having 60% or more tree canopy cover

6 Low elevation here is defined as no more than 1000-1700' above sea level depending on latitude and microclimate (DeMeo et al. 1992).

7 Woodland refers to an open savannah-like forest in which tree canopy cover is 25% or less (Viereck et al. 1992)

8 In part. Some of these forests can develop closed canopies and would be lumped into the low elevation sitka spruce series for the R10 classification. This is due to consideration of spruce as a disturbance-dependent species (DeMeo et al. 1992).

Thanks to Paul Alaback for assistance with this comparison of forest-type classifications.

TABLE 2. Comparison of the forest habitats described in this report with the structural classification of Caouette and DeGaynor (2005).

Units of conservation concern described in this report	Equivalent units in the size/density (SD) classification (Caouette and DeGaynor 2005)
riparian large-tree spruce	SD-67
karst large-tree	SD-67
upland hemlock/spruce	SD-4H, SD-4N, SD-4S, SD-5H, SD-5N, SD-5S, SD-67
cedar/hemlock	SD-4H, SD-4N, SD-4S, SD-5H, SD-5N, SD-5S, SD-67
young, even-aged conifer	SD-4H, SD-4N, SD-4S, SD-5H, SD-5N, SD-5S, SD-67
wet, small-tree	SD-4H and non-POG types

Well-drained, Low-elevation Habitats

In Southeast, forest is the dominant habitat on most well-drained surfaces below alpine elevations. But there is considerable variation in soil drainage within these forest habitats, which influences nutrient availability, temperature and rooting depth for plants. Drainage is the principal environmental factor determining both overstory and understory species composition. Poorly drained forested sites have open canopies, thus drainage indirectly exerts control on light penetration to the understory.

Soil drainage is largely a function of the mix of particle sizes in the substrate–boulders, cobbles, gravel, sand, silt, and clay–as well as the movement of ground water. These particles are the legacies of land-forming agents such as rivers and glaciers (Fig 4).

The sorted (similar sized) particles left by streams and rivers (alluvium) result in well-drained substrates that support the most productive forests. In contrast, glaciers leave *unsorted* particles of all sizes from boulders down to clay, resulting in intermediate drainage conditions that grow forests of more modest size. At the other extreme, the fine sediments of pond- and lake-beds are poorly drained, supporting wetlands and eventually accumulating the deep peat deposits of bogs and fens.

Because old growth is the habitat of greatest conservation concern in Southeast, the following descriptions of terrestrial habitats begin at this successional end point. Discussion of the successional stages that lead to this habitat on well-drained (non-wetland) surfaces follows in the next section.

DEFINITIONS OF OLD GROWTH FOREST

Old-growth forests take dramatically different forms in different bioregions, and it has been challenging to come up with widely applicable definitions. Within Southeast, old-growth forests also

FIG 6. Contrasting forest types on northern Kosciusko Island. The smooth-textured forest in upper left is an even-aged stand recovering from clearcut logging. Bluish-green color suggests mostly spruces. The ragged canopy in lower right is highly productive old-growth hemlock-spruce forest with large canopy gaps and many snags at varying stages of decay.

differ notably, responding especially to soil drainage and elevation as noted above. After many centuries there may be some convergence toward a more similar stand structure on upland versus alluvial sites, but clear differences remain in species composition, canopy structure, and wildlife values even after millennia of change.

Forest succession has no tidy, predictable "outcome." Certainly, there is no sudden threshold age after which a forest fully and ever afterward qualifies as old growth. Given the continuous nature of succession, Spies and Franklin (1988) proposed an index of "old-growthness," which is perhaps more reasonable than trying to identify one point on a spectrum of change.

The following simple description of old growth can be applied to the Southeast rainforest in general. A more technical description also is provided.

Old-growth forest includes old trees. In Southeast, the oldest trees may exceed 1,000 years of age.

Dominant trees typically exceed 300 years of age. One key characteristic of old growth is that it includes trees of multiple ("uneven") ages and sizes, from seedlings and saplings to pole-sized trees (30–80 years) to trees many centuries old (Fig 7). Such forests have often developed over millennia.

But old growth isn't static. Some scientists have described old growth as dynamic steady-state forests. When individual trees or groups of trees blow down or die, a gap in the forest canopy is created and new trees and other understory plants compete for light and resources in that new space. This dynamic process results in great diversity of tree ages and sizes.

The holes, or gaps, in the overhead canopy allow sunlight to penetrate to the forest floor, resulting in a rich understory of herbs, ferns, and shrubs. Old growth is also structurally diverse, with multi-layered canopy and wide variety of tree size and spacing.

Old growth has an abundance of standing snags and decaying logs on the ground and in streams. These snags and logs provide important habitat for fish and wildlife. An abundance of lichens and fungi also play key roles in old-growth nutrient cycling.

Forest ecologists require more technical definitions of old growth for both "conceptual" and "working" applications. *Conceptually*, old growth is a forest governed by "gap dynamics," a term referring to the patchy mortality of dominant trees and all ensuing consequences of tree death (Wells et al. 1998). Only with this mortality do microclimate diversity, understory reinitiation, multi-cohort age composition, and the richer understory species diversity of old growth occur.

Practical measures of these conceptual features are elusive, however. And in the real world, quantitative

FIG 7. Two extremes in old-growth forest composition on Prince of Wales Island. Above is a scrubby stand of lodgepole pine, yellow-cedar and western hemlock on wet soils at Kasaan Bay. Below is the highest scoring Landmark Tree site on northern Prince of Wales (see Landmark Trees Project, pg 15). Note the better-developed understory on the scrubby site where more light is available.

Both habitats have ancient trees and fully qualify as old-growth forest.

FIG 8. Ecological characteristics of old-growth forests from Franklin & Spies (1991)

Structural:
1) wide range of tree sizes and spacing
2) large trees for species and site
3) decadence in large older trees
4) presence of large snags and down logs of varying decay classes
5) canopy gaps
6) understory patchiness
7) high organic matter accumulations
8) multiple canopy layers

Compositional:
1) high diversity of plant, vertebrate and invertebrate communities
2) richer and more productive arboreal and understory plant communities than in younger forests
3) high habitat diversity

Functional:
1) distinctive nutrient and hydrological cycles
2) slow growth of dominant trees
3) stable biomass accumulation.
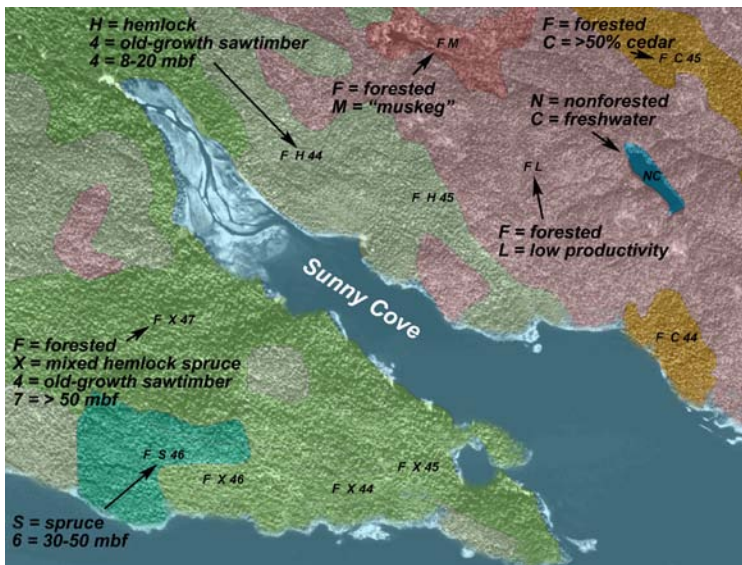
FIG 9. Example of 1977 TIMTYP polygon codes at Sunny Cove, Cholmondeley Sound, Prince of Wales Island.

In the code "F S 47," the first "F" indicates forest. "S" means spruce dominated. "4" stands for sawtimber, the largest of 4 tree-size classes. And "7" is the largest of 7 stand-volume classes.

Although mapped by experienced foresters, systemic inaccuracies have been demonstrated in the volume assignments–the last number in the forest type codes.

definitions are a necessary foundation before the distribution of forest types can be mapped and management decisions can be applied.

Researchers in Southeast have found that simple graphs of tree age and size distribution show clear differences between old and second growth (Fig 10). Old-growth trees develop heavier, craggy limbs, and epiphytic lichens reach higher diversity and biomass than in younger, even-aged stands (Nowacki and Kramer 1998).

But even these quantifiable parameters cannot provide a *working* definition of old growth across the vast landscape of Southeast. Thorough ground-based mapping is impossible at this scale, and interpretation instead must rely on attributes detectable on aerial photographs and other remotely acquired imagery. Of course, ground-truthing of small sample areas is essential for improving the accuracy of interpretations from imagery, but forest-type mapping is by necessity mostly "site unseen."

Examining the intricate mosaic of forest types on maps such as Fig 9 reveals important patterns at many scales, from watersheds to biogeographic provinces
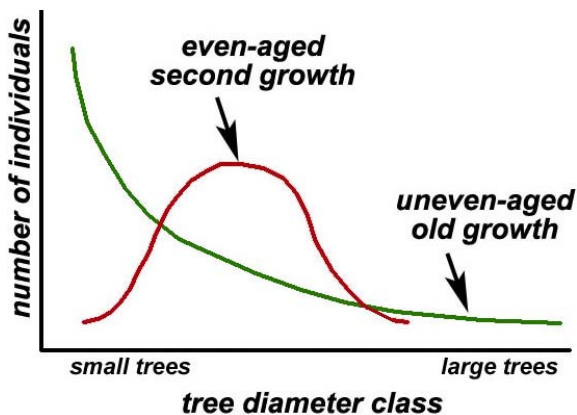
FIG 10. Size distributions in young versus old forests. The top of the "bell curve" in younger forests results from crowding of same-sized trees. Old forests have a wider range of tree sizes, and because the fewer large crowns are positioned at different levels, more light is admitted to the understory.
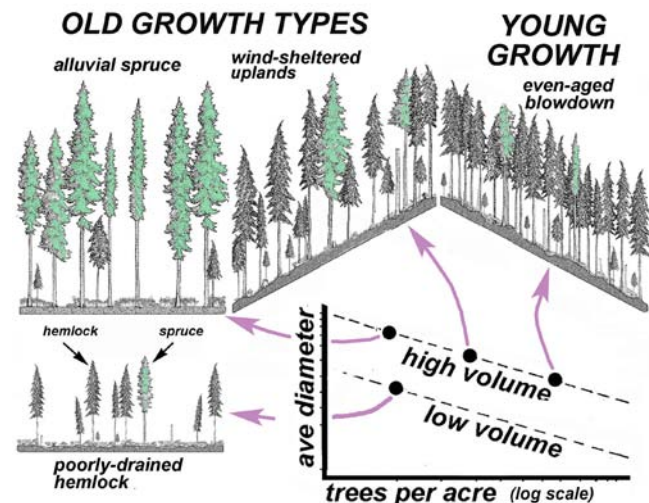
FIG 11. The relationship of tree size (average diameter) and density (trees per acre) effectively describes a wide range of structural variety. With age and mortality, tree density decreases. Shown on the left are 3 very different types of old growth: large trees at low density typical of alluvium, small trees at low density typical of wet soils, and medium size trees at medium density, exemplified by upland hemlock forests.

FIG 12 Contrasting high volume stands.

Stand A: Mature, even-aged spruce, probably 120 to 150 years old, on south-facing hillside above Starrigavan Creek near Sitka. Tight spacing of medium-sized trees results in very high volume. Landmark Tree investigators measured 128,000 gross board feet in this acre (.4 ha). This type of mature windthrow stand dominated by spruces typically results from severe blowdown that uproots many of the original trees, exposing mineral soil and giving the advantage to spruce seedlings. These stands have very high timber values but low habitat diversity and often support little understory because of the interlocking canopy of same-sized trees.

Stand B: Although this alluvial-fan spruce forest on western Chichagof has much bigger trees than stand A, wider tree spacing results in considerably less volume: 70,000 gross board feet per acre. Wide canopy gaps allow high understory production—high habitat value.

to the entire Southeast ecoregion. Old-growth forests provide wildlife habitat features that are unavailable in open wetlands or younger even-aged forests. Comparing the mosaic of land cover on Research Natural Areas (protected ecological research areas designated by the USFS) between southern Southeast and Prince William Sound, Alaback and Juday (1989) noted that the patch sizes of old growth declined northward. This latitudinal gradient has implications for conservation of wildlife habitat.

Four types of old-growth forest are described below. Distinctive conservation issues are associated with each type. A fifth type, the wet, small-tree old-growth, is discussed in the section on poorly-drained habitats. This segregation of types is a rather arbitrary separation of what could be considered a continuum of forest types responding to subtle differences in soil drainage. It reflects the difficulty in clearly distinguishing between some habitat categories. One primary criterion in habitat classification is "mappability"; it is difficult to build conservation strategies for habitats that cannot be delineated on a map. Therefore, the organization below adheres as closely as possible to habitat distinctions as treated by available GIS data layers.

Tree Size and Density

The choice of measures to characterize forest structural diversity is a critical prelude to forest type mapping. After prolonged study, the USFS (Caouette and DeGaynor 2005) selected the relationship of tree size (mean diameter at breast height) to tree density (trees per acre [ha]). With these 2 metrics alone, all forest types in Figure 11 can be characterized. Although site productivity eventually places limits on tree size and spacing in old-growth forests, mean diameter consistently increases while density decreases over the first few centuries of succession (Fig 12). The size/density relationship has also been identified by workers in the Pacific Northwest as an effective measure of forest stand structure (Spies and Franklin 1991).

Size and density of trees are both accessible to mapping from aerial photographs. All 4 forest types

shown in profile view in Figure 11 can easily be delineated from vertical stereo photography. The entire Tongass National Forest has been mapped by such photointerpretation (*Mapping Forest Structure* sidebar), resulting in the TIMTYP GIS layer. But the TIMTYP polygons only purport to show stand volume, not tree size or density. Clearly, a better map is needed that actually delineates forest types according to mean size and density. Ultimately, new technologies such as lidar will give us radically improved forest structure maps, but such maps are not expected to be available for at least several more years.

In the meantime the challenge is to "distill" a useful tree-size map (or a tree-density map) from the original TIMTYP database. Considering that the volume-class (VC) portion of the code was derived in large degree from photo-interpretation of canopy texture and tree height, could the VC designation actually provide a valid measure of mean tree size in the larger-diameter classes? Field data suggest that it can (J. Caouette, Statistician, USFS, Juneau, AK, personal communication 2005).

The USFS conducted 2 grid-based inventories of Tongass timber in the 1980s and 1990s. Hundreds of plots were visited and assessed for tree species, height, diameter, crown depth and spread, disease, and stem density. Also recorded were soil type and understory plant composition. Ground-truthed data plotted against photointerpreted TIMTYP codes can be compared to actual mean tree diameter with the assigned VCs. The combined VCs 6 and 7 give a 69% probability of encompassing forests with mean diameter greater than 21 in (53 cm). (J. Caouette, Statistician, USFS, Juneau, AK, personal communication 2005)

As of 2006, the most useful GIS coverage for most forest analyses is the tree-size map (Fig 13). As with the 1997 volume strata map from the USFS *Tongass National Forest Land and Resource Management Plan (*TLMP), this map separates only 3 volume classes within the POG.

But whereas the 1997 volume map lumped 40% of the POG in the highest volume stratum, the "large-tree" class in this newer tree-size map includes only the top 11% of the POG. Therefore, the large-tree class is a more exclusive class, and better identifies a rare and much diminished forest type that has high ecological values. Proportions of large-, medium-, and small-tree forests in Figure 13 are fairly representative of their distribution Tongass-wide.

The tree-size map is only a predictive model. It is not accurate enough to be used at fine scales for timber sale layout within watersheds. (For example, small patches of large trees <10 acres [4 ha] are often not mapped.) But the tree-size map is well suited for comparisons of relative tree-size potential among watersheds. For purposes of this report, the tree-size map is a valuable, science-based interim tool for assessing ecological values of individual watersheds within biogeographic provinces of Southeast.
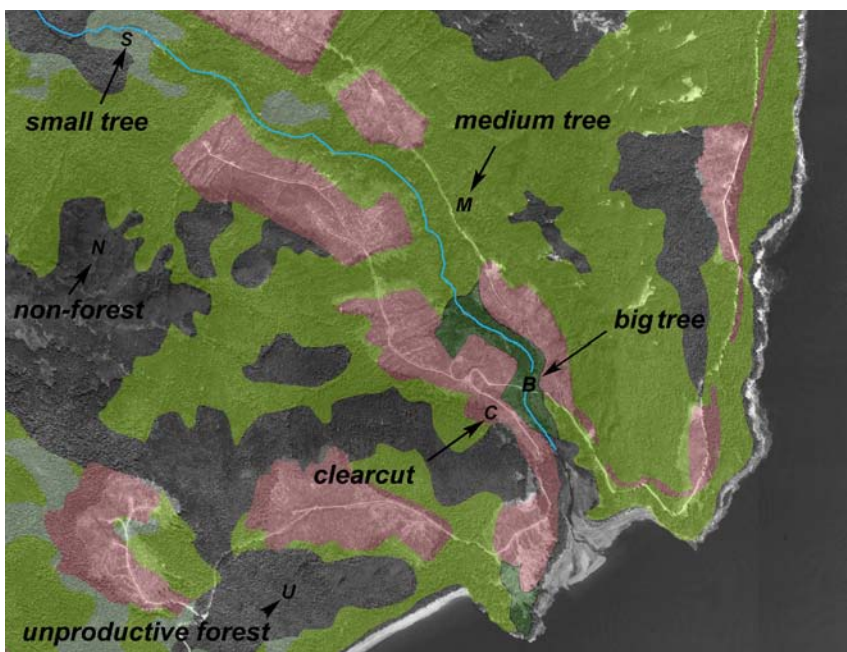
FIG 13 Tree-size map, a derivative of TIMTYP and other GIS layers. Wukuklook Creek, Chichagof Island. This map merges former volume classes 6&7 to create a "large-tree" class. It offers a ground-truthed 69% probability of mean tree diameter greater than 21 inches (53 cm). Individual trees in these large-tree old-growth stands may grow to over 6-8 ft (1.8-2.4 m) in diameter.

Mapping Forest Structure

The history of forest type mapping for the Tongass National Forest is complex and far from concluded. The successive iterations of USFS forest type maps are well documented in Caouette and DeGayner (2005). This brief look at mapping reviews its evolution, pitfalls encountered, and attempted resolutions.

The first generation of forest type maps for Southeast was created by skilled photointerpreters in 1977. Called "TIMTYP," this map or GIS layer consists of 240,000 polygons averaging 60 acres (24 ha) in size and identifies both forest and nonforest habitats (Fig 9). Forested types are separated into non-productive old growth (<8,000 net board feet per acre [nbf/a]) and Productive Old Growth or "POG" (>8,000 nbf/a, about 1/3 of the Tongass). Productive forests are further classified by dominant species, tree size, and volume class (VC).

Stand volume proved to be one of the most difficult forest attributes to delineate from aerial photography. Tongass-wide field inventories conducted in the 1980s and 1990s demonstrated statistically little difference between stands mapped as VC 6 and 7. Also, considerable acreage of very high-volume forest is found within polygons mapped only as VC 5. This result occurs because mature second-growth forests with high density of tall, medium-diameter trees frequently contain well over 50,000 nbf/a; however, their closed canopy makes them hard for photointerpreters to differentiate from shorter, lower-volume stands.

The TIMTYP maps, for want of better alternatives, have been the standard measure of forest habitat quality for the past quarter century. Ranger districts used them to plan and defend timber sales. Researchers used them in wildlife studies. And conservation groups used them in advocacy and litigation. The Tongass Timber Reform Act of 1990 attempted to protect forest diversity by mandating "proportionality"—logging in proportion to the availability of VCs.

Soon afterward, a 1994 lawsuit by The Wildlife Society concluded in the judgment that TIMTYP VCs "represented arbitrary and capricious information for meeting requirements of the proportionality law" (Caouette and DeGaynor 2005). This ruling set about a protracted series of reassessments and statistical analyses by the USFS that is still ongoing a decade later.

The first revision of TIMTYP collapsed VCs 5, 6, and 7 into one class, with 3 levels of distinction: low, medium, and high (Julin and Caouette 1997). This 1997 timber-volume map from the TLMP (USFS 1997) was criticized by wildlife biologists who felt that lumping 40% of the POG into the high stratum reduced their ability to identify big-tree old growth that was considered rare and valuable habitat.

But the problem was more fundamental than the contracted range of VCs. A flawed common vocabulary has emerged from decades-long dependence on the TIMTYP maps. Foresters, conservationists, and wildlife researchers alike have all used the term "high volume" not only in the valid sense of commercial timber quantity, but also to indicate the most ecologically valuable stands of big trees. Unique to Southeast, this volume language is not employed elsewhere in temperate rainforest environments. Volume alone—whether accurately mapped or not—tells little about forest structure. A more meaningful dialog on forest issues needs to build on better measures of forest structure such as the relationship of mean tree size to density.

Although TIMTYP has serious shortcomings for measuring timber volume, it does identify forest structural differences of ecological relevance (Caouette et al. 2000). Researchers, land managers, and conservationists all need a better forest map. Interim solutions will continue to depend on combinations of TIMTYP with other available data layers such as common land unit (CLU) and the NWI. Such a combination was used to develop a tree-size map for Southeast shown in Figure 13.

Rapid advances are being made in forest structural mapping from lidar and other remotely acquired imagery. Lidar penetrates forest canopies to produce detailed maps of tree diameters, branch sizes, foliage layers, and ground contours. High expense currently limits this technology to experimental coverages of small acreage, but prices are falling as accuracy improves.

According to old-growth researcher Paul Alaback, ". . . the real issue throughout the rainforest zone is the need for a land mapping classification that matches the ecological concept of old growth. The size-density relationships are also just an approximation of the 4-5 factors that define most old growth types. The excitement about lidar is that not only can it tell us densities and sizes of trees but also canopy complexity, canopy heights, and patchiness of canopy cover - the key attributes that define old growth function." (P. Alaback, forest ecologist, University of Montana, personal communication, 2006)

UPLAND HEMLOCK/SPRUCE FOREST

Throughout Southeast on moderately productive upland slopes of till and bedrock, western hemlock-dominated old growth prevails (Fig 14). These stands usually include small amounts of Sitka spruce, and, sometimes, red- or yellow-cedar (*Thuja plicata* and *Cupressus nootkatensis*, respectively). Broadly defined, this forest type is by far the most common in Southeast. Tables 1 and 2 compare forest types described in this report with other USFS classifications based upon species composition and stand structure, respectively. Depending on elevation, drainage, and other secondary influences, the hemlock dominated old growth may range from low to high productivity, but we consider it here to fall exclusively within the Productive Old Growth (POG). Non-productive, scrubbier forest types are described later in the section on wet, small-tree forest.

Forest Structure

Shade tolerance explains why the upland old-growth forest of Southeast tends to be dominated by western hemlock (and in some areas western redcedar). Hemlock and redcedar are better adapted than spruce, yellow-cedar, or shore pine (*Pinus contorta*) to growing up beneath a shaded forest canopy. Therefore, over the course of several centuries, composition of the high canopy shifts strongly to hemlock, which typically composes 70% to 80% of Southeast forest stands by volume (Harris and Farr 1979) (Fig 16).

Sitka spruce usually continues to be an important secondary element of these forests. In spite of shade intolerance, spruce may persist for millennia in hemlock-dominated old growth. One key to perpetuation of spruce even in the absence of major disturbance seems to be the repeated small-scale exposure of mineral soil on mounds created by windthrown trees (Fig 17). This available soil may allow continued recruitment of spruce saplings, some of which eventually survive to come up through gaps in the forest canopy (Deal et al. 1991).

Some features of hemlock old growth are illustrated in Figure 15. The view is from the side of a 1-acre (0.4 ha) block, about 200 ft (60 m) wide. Tallest trees are 130 ft (40 m). Trees of all sizes and ages are present. Although western hemlock

FIG 14 Productive hemlock old growth near Naukati, northern Prince of Wales Island. All trees in this view are western hemlock, including the dense sapling regeneration. Large snag on left provides habitat for cavity nesters and denning habitat for black bears..

dominates both in numbers of individuals and volume, the 2 largest (and possibly oldest) trees in the stand are Sitka spruce. In shadier microsites, only hemlocks are able to slowly grow up beneath the canopy. Two small spruces have become established in well-lit canopy gaps, but they may not survive if the gaps fill in with taller hemlocks. The forest has abundant standing and down dead wood in all stages of decay, providing nutrients for burrowing arthropods, hiding cover for small mammals, and soft wood for cavity excavators and secondary hole-dwellers like small forest owls. Understory shrubs form a patchwork in response to variable light penetration. Heart rot, fluting, and mistletoe make the old hemlocks valuable to wildlife but unattractive to loggers. If this stand were logged, the 2 large spruces would provide most of the economic value.
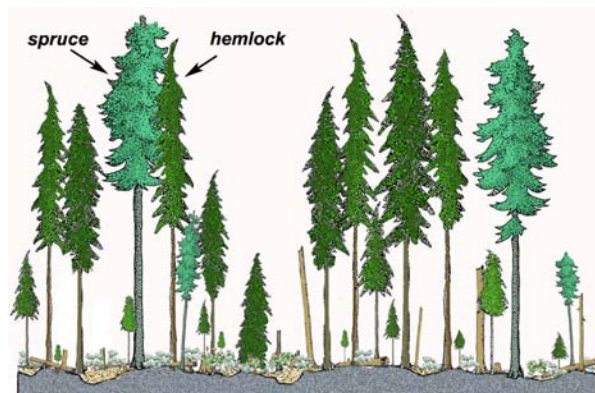
FIG 15 Conceptual profile of upland hemlock old-growth. Note the uneven age structure, gappy canopy, snags and down logs, and productive understory development characteristic of old growth.

The oblique canopy view in Figure 16 shows a forest quite similar to the conceptual profile in Figure 15. Spruces are a minor component of this hemlock-dominated stand. Trees are generally well spaced, and the large gap in the lower right admits light to a productive understory plant community.

In tall old-growth forests, huge gradients in moisture and light exist between the treetops and the understory shrubs. This disparity results in much wider diversity of niches for birds, invertebrates, and epiphytes such as lichens than can be found in younger forests with simpler canopies (Spies and Franklin 1988). Large branches form only on trees with slow height growth (>200 years old). Large branches provide important nesting sites for marbled murrelets (*Brachyramphus marmoratus*) and other birds and are also a critical element for the snow interception provided under the old-growth canopy. These branches are important even after their demise. When they eventually break off from heavy snow loading, the branches create fungal entry points and rot, providing ideal habitats for many birds and mammals (P. Alaback, Forest Ecologist, University of Montana, Missoula, personal communication 2005). The witches-broom deformities caused by hemlock dwarf mistletoe infestation also provide important habitat for birds and flying squirrels (*Glaucomys sabrinus*).

Although these old-growth forests in relatively wind-sheltered locations can persist for millennia without stand-replacing disturbances, single-tree and small-patch blowdown is endemic in all Southeast forests. After many centuries of uprooting by wind, the forest floor develops a mound-pit topography (Fig 17). The unique rooting environments on these windthrow mounds are more common in Southeast than farther south in the Pacific Northwest (Deal et al. 1991).

Bormann et al. (1995) estimated that these pits and mounds made up an average of 42% of the surface of old-growth stands studied in northern Southeast. The amount of soil carbon in a forest varies with frequency of windthrow-induced soil disturbance that brings these nutrients up to the surface. Therefore, mound-pit topography has important consequences in forest succession. Diseases that cause trees to snap, rather than uproot, can reduce or eliminate windthrow

FIG 16 Canopy view of productive hemlock old growth near Trout Creek on Kosciusko Island. Arrows indicate the two largest spruces; others can be found by searching for the paler grey-green foliage. Recently dead snag in center retains fine brances. Note the ragged, broken canopy characteristic of old growth, which allows sunlight to penetrate the forest and support a diversity and abundance of understory plants.
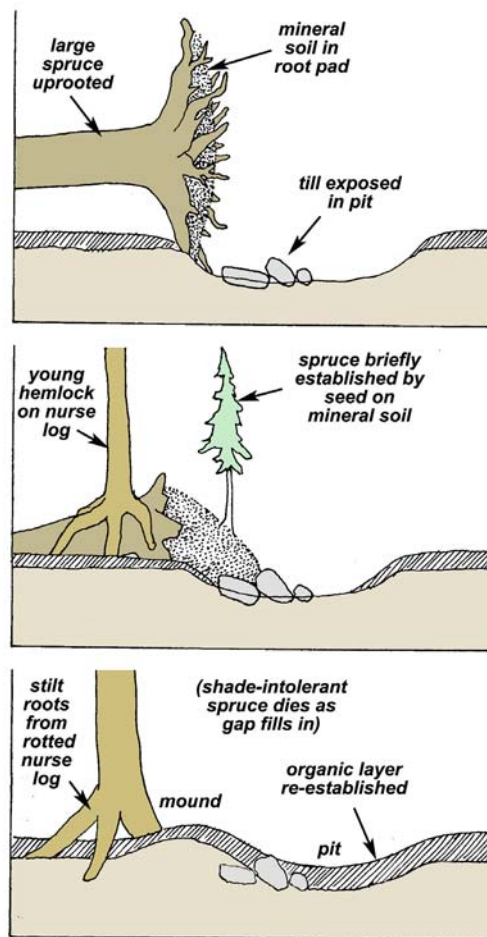
FIG 17 Below left: Development of mound-pit topography in old-growth forest. After Bormann et al. (1995)

disturbance and mound-pit formation, leading to thick organic soil horizons and downward trends in forest productivity. The ratio of spruce to hemlock also declines, because spruces establish best on exposed mineral soil.

Understory Plant Community

The dominant shrubs of upland hemlock old growth are blueberries and huckleberries of the genus *Vaccinium*, along with rusty menziesia (*Menziesia ferruginea*). Under well-lit gaps, more light-demanding shrubs like salmonberry (*Rubus spectabilis*), devil's club (*Oplopanax horridum*), and red elderberry (*Sambucus racemosa*) may occur.

Herbs of the forest floor could be divided into the tender-leaved species that wilt in fall and the evergreens that persist even under snows throughout the winter. Examples are shown in Figure 18. Of these, the species most important to wintering deer are bunchberry (*Cornus canadensis*), five-leaved bramble (*Rubus pedatus*), and fern-leaved goldthread (*Coptis asplenifolia*) (Hanley and Brady 1997). It should be noted that these species are relatively uncommon in the forest of large riparian spruces, where devil's club, salmonberry, and foamflower (*Tiarella trifoliata*) are the typical understory. It would be fair to call upland hemlock old growth the "deer forest," and riparian spruce old growth (described below) the "salmon/eagle/bear" forest.

Wildlife

The importance of hemlock old-growth to wildlife—especially Sitka black-tailed deer—has been well studied. Researchers have measured a negative correlation between winter snow depth and tree size (Hanley and Rose 1987, Kirchhoff and Schoen 1987). Scrubby forests with small,

widely dispersed trees accumulate deep snow in hard winters, making access for deer difficult. At these times, optimum foraging is found in large-tree upland old growth (Schoen and Kirchhoff 1990). Only complex, multilayered canopies and large branches combine snow interception in winter with adequate penetration of sunlight for the growth of forage plants (Kirchhoff and Schoen 1987). Figure 47 demonstrates this relationship between sunlight penetration and understory growth, as can be seen from comparing the canopy of block E to the preceding even-aged closed canopies in blocks B through D.

Telemetry studies by the Alaska Department of Fish and Game (ADF&G) showed that deer selected habitats with large-tree old growth on south-facing slopes below the 1,000-ft (300-m) elevation (Schoen and Kirchhoff 1990). When snow cover on the ground in forest openings exceeded 6–12 inches (15–30 cm), deer moved into the largest upland large-tree stands within their home ranges.
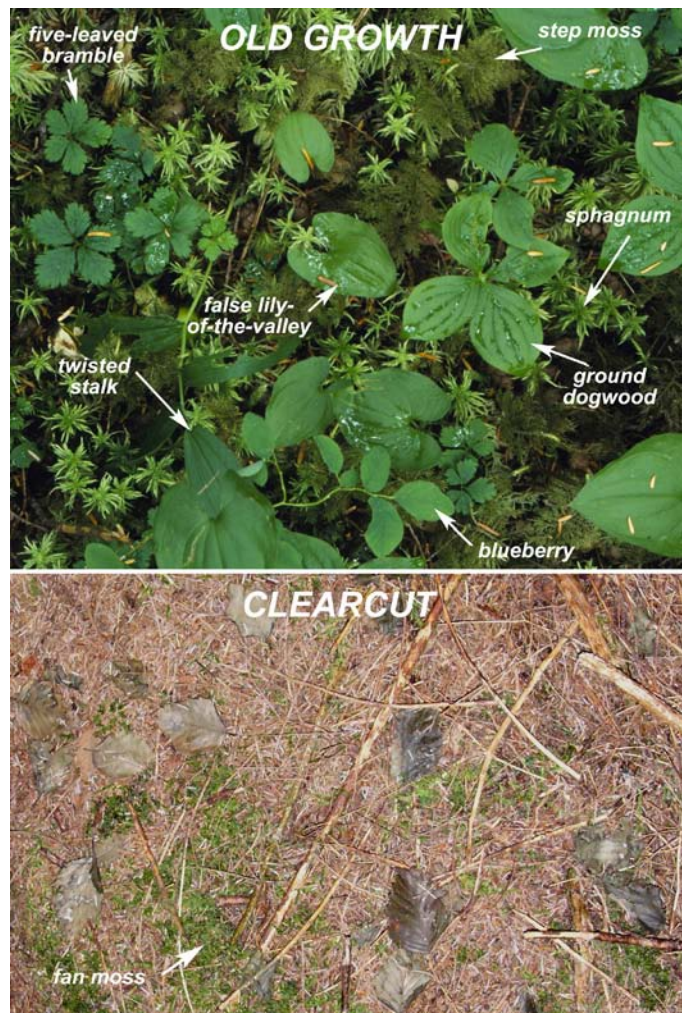
FIG 18 Comparison of the "forb layer" in old and young forests.
   Above: Common herbs and mosses of the upland hemlock old growth. Twisted stalk (*Streptopus roseus*) and false lily-of-the-valley (*Maianthemum dilatatum*) provide summer deer food but wilt in the fall. Bunchberry and five-leaved bramble stay green all winter and provide critical forage. Mosses, including step moss (*Hylocomnium splendens*) and sphagnum (*Sphagnum girgensohnii*), are little used by wildlife.
   Below: The above plants aren't available in shady cutover forests dominated by young conifers. Only inedible mosses like *Rhizomnium glabrescens* and *Plagiothecium undulatum* grow in scattered tufts amongst twig and needle litter.

LANDMARK TREES PROJECT

The Landmark Trees Project is an effort to find, describe and understand the most magnificent forests of Southeast. Founded in 1996 by Sam Skaggs of Alaska Research Voyages, Inc., the project has documented 75 superlative 1-acre (0.4-ha) stands across the Tongass as of 2006.

LT forests are scored according to the dimensions of the largest tree and the wood volume of the surrounding acre. They are also assessed for ecological values such as bear habitat. The project, described at www.landmarktrees.org, involves residents all over Southeast who seek deeper familiarity with their backyard treasures.

The LT-caliber forests are the cream of the cream, the finest 1% of the big-tree forest. They grow on 2 basic landforms: karst and alluvium. Although karst once held the greatest forests in Alaska, so few remain that the great majority of LT sites are alluvial.

Most LT sites are far from towns. They're usually on salmon streams—very sensitive habitat for animals like brown and black bear. Another category of assessed big-tree plots is known as Community Landmark Tree Stand. At Ketchikan, Petersburg, Sitka, and Kake, these sites are quickly reached on trails and are good places to learn about giant spruce forests of Alaska. Interpretive booklets map every tree in the acre, describing the ages, physical dimensions, and history of individual trees.

"Landmarkers" have come to feel that the association of spruce, salmon, bear, eagle, devil's club, and alluvium defines the core terrestrial community in the Tongass.
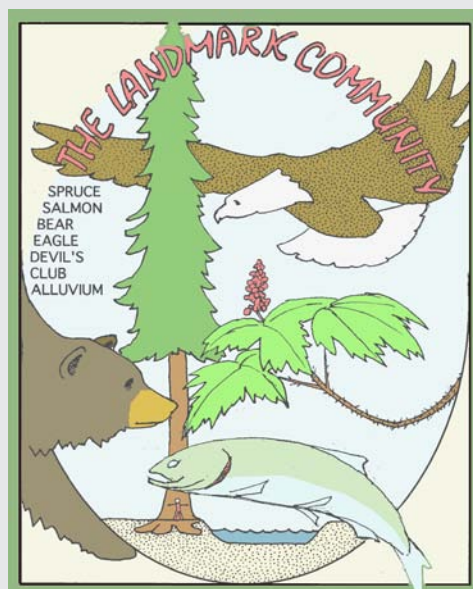
Succession in Landmark Tree forests

Many LT stands are barely mature enough to be considered "old growth." Such stands are often 90% spruce by volume. Trees reach 200 ft (61 m), with full, undamaged tops, yet rarely exceed 5 ft (1.5 m) in diameter at 10 ft (3 m) up. Large canopy gaps foster nearly complete cover of devil's club/salmonberry thickets. Some gravel/cobble surfaces are flooded annually.

In "middle age," a third of the volume may be hemlock. Tree height and volume peak. On the finest alluvial LT forests, volume hits a plateau in middle age at about 140 mbf. Largest diameters are about 7 ft (2 m) across at 10 ft (3 m) up. Blueberry joins devil's club in the understory, where flooding now occurs less than once per century.

Truly ancient LT sites are extremely rare.Stream incision has left the floodplain inactive for millennia. Hemlock is ~70% of stand volume, but enormous old spruces persist. By the time an Alaska spruce reaches 8 ft (2.4 m) diameter at 10 ft (3 m) up, its top is usually broken. Deeply furrowed bark suggests an age approaching 1000 years, but increment borers can't reach the pith of such trees.
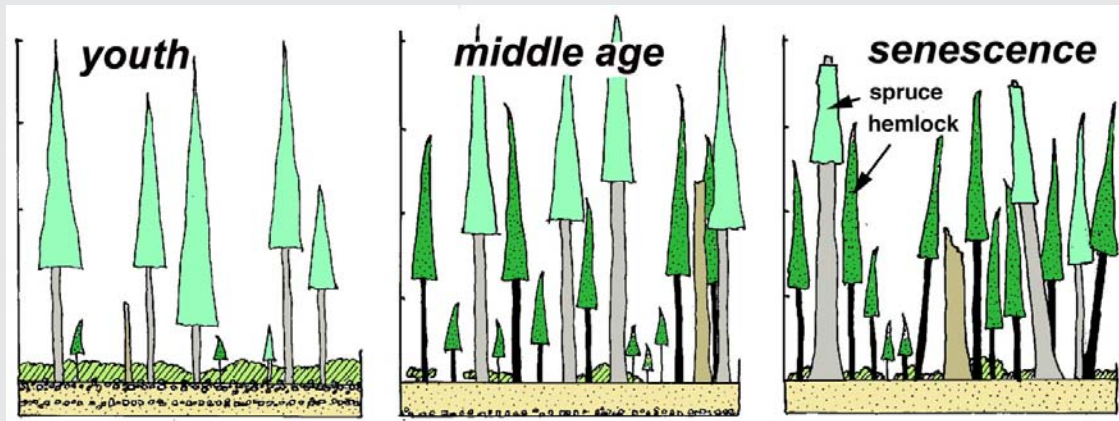
On ranges where carrying capacity is overtaxed, even forage species normally avoided like rusty menziesia and spine-defended devil's club are eaten. This forage consumption results in a distinctive, almost shrubless forest understory in mild-winter, outer-coast environments lacking wolves, like west Chichagof and Coronation islands. At these densities, deer also severely curtail the reproduction of forest conifers.

Relationships of other wildlife species to upland hemlock old growth are discussed in later chapters. One species for which this forest type provides essential habitat is the marbled murrelet, which nests in old-growth forest. This species needs wide lateral branches with abundant moss to support its simple cup nest, merely a depression in arboreal mosses such as *Antitrichia curtipendula.* For more information on murrelet habitat relationships, see chapter 8.

RESULTS OF "QUICK-CRUISE" SAMPLING: DISTINCTIVE WILDLIFE VALUES OF UPLAND VERSUS RIPARIAN FORESTS.

Deer researchers Matt Kirchhoff and Tom Hanley have developed a quick-cruise sampling protocol, by which winter deer habitat can be given a score. Half of the score comes from the availability of winter forbs and shrubs; the remainder comes from attributes influencing the amount of snow that accumulates: slope, aspect, elevation, distance from beach, and ability of the canopy to intercept snow.

Landmark Tree researchers have applied the deer quick cruise to the great riparian spruce forests across Southeast. These forests flunk the test for deer winter range. Understories are usually devil's club and foamflower, rather than the blueberry, ground dogwood, and trailing raspberry that deer prefer. The well-dispersed spruces with "starry" radiating branching patterns (Fig 22) also allow more snow to build up on the ground than does the denser foliage of upland hemlock stands. Adding to

that effect, the streamside bottomlands often collect cold air, preserving the snow pack and placing these habitats off limits to deer for much of the winter and spring.

Deer do seek out the succulent riparian herbs in spring and summer. But the classic riparian Landmark Forest is best characterized as the spruce-salmon-bear-eagle-devil's club-alluvium association (see Landmark Trees sidebar). To score this forest, Landmarkers developed a riparian bear habitat assessment. A perfect-scoring late-summer bear habitat has a heavy pink or chum (*Oncorhynchus keta*) run with shallow fishing riffles, bordered by an open-canopied alluvial spruce forest over dense thickets of fruiting devil's club, salmonberry, and stink currant. Unlike the perfect winter deer forest, the ultimate late-summer bear forest is more than a mile (1.6 km) from the beach, beyond the range of most hunters and tourists. This distance from beach access is typical of many of the greatest remote Landmark Tree sites.

The upland hemlock old growth is a slow-growing community that "hangs on" to its production. Structural complexity makes it an important habitat for many animals in the lean times of winter. In contrast, the riparian spruce forest could be called an "exporting community" in the sense that animals of surrounding communities haul away its summer production. Small in area compared to the upland forest, the riparian spruce forest is important far out of proportion to acreage for many kinds of wildlife, including the hunters and scavengers of salmon, berry-pickers, insectivorous birds, and summer grazers.

FIG 19 Nossuk Creek, Prince of Wales Island. This great bear stream has spawning runs of pink and chum salmon.

RIPARIAN (ALLUVIAL) LARGE-TREE SPRUCE FOREST

Two of the forest types described in this report are termed "large-tree:" the riparian forest of large spruces and the mixed-conifer forest on karst bedrock. Each of these forest types falls within the highest size/density class (SD-67) of Caouette and DeGaynor (2005). Tables 1 and 2 show the relationships of these forest types according to other existing classifications. The "large-tree" class is defined as having greater than 21 inches (53 cm) quadratic mean diameter sustained over a minimum of 25 acres (10 ha). Both the riparian large-tree spruce forest and the karst large-tree forest are only subsets of habitat units as defined by other forest-type classifications But they have extremely high habitat values and have been disproportionately logged, thus deserve special attention in a conservation assessment.

The largest trees in Alaska grew on 3 basic landforms: alluvium, colluvium, and karst. Alluvium and colluvium are surficial or "unconsolidated" deposits. Karst is a bedrock substrate developing on limestone and marble, described in the following subsection.

Alluvium

In some ways it's more appropriate to refer to the streamside large-tree forest as "alluvial" rather than by the more inclusive term "riparian." A riparian forest is simply any forest that interacts with a stream. It provides shade over the channel, sheds leaves and arthropods into the water, contributes structural diversity to aquatic habitats in the form of fallen logs or root masses, and *sometimes* benefits from proximity to the stream. But on small headwater streams on gullied slopes, the rooting environment for a riparian tree may not be qualitatively different from that of upland slopes remote from any channel; tree size may be unremarkable. The large-tree streamside forest is usually found farther downstream, where alluvial deposits frame the channel.

Alluvium is sorted sediment deposited by moving water. Because fine, drainage-impeding silts and clays are deposited only by still water, they are not a large component of most alluvial surfaces. The coarser sand, gravel, and cobbles of alluvial deposits allow for good soil drainage, root aeration, and optimum tree


FIG 20 Raw alluvial fan in upper Glacier Bay, constructed by rapid erosion of unstable upland slopes in a few decades since the site was uncovered by the receding Muir Glacier. In 400 years, a large-tree spruce forest may stand on this fan. The upland slopes may have old-growth hemlock forest of more modest size.

growth. Stream sediment is also more nutrient-rich than the glacial till covering most upland slopes.

Alluvial landforms include flood plains and fans (Fig 5.1.14). Flood plains are constructed over the course of millennia by repeated overbank deposits of streams and rivers. Alluvial fans are created where streams come off steep slopes onto gentler ones. Forests on both of these landforms contain some of the largest spruces in Southeast.

Flood-plain dynamics are described in Section 5.2. On the most active flood plains like Taku River, where overbank floods are annual or decadal events, conifers may have difficulty establishing. There, a more flood-tolerant forest of cottonwood (*Populus trichocarpa*), alder (*Alnus spp.*), and willow (*Salix spp.*) prevails. With decreasing frequency and severity of flooding, Sitka spruce and eventually western hemlock colonize the alluvium. On the lower, gentler reaches of many Southeast streams, moderate levels of fluvial (stream action) disturbance maintain spruce dominance by preventing colonization of hemlocks. As discussed above, the more shade-tolerant western hemlock may come to dominate on very stable surfaces after many centuries. But long-lived spruces, towering 50 ft (15 m) over the tallest hemlocks on rich riverbanks, can hold out indefinitely with only a flood or 2 per millennium to "reset the clock."

Alluvial fans are common in the mountainous regions of Southeast and absent from flat country or gently rolling hills. When a steep-gradient stream meets a more level surface—such as a flood plain in
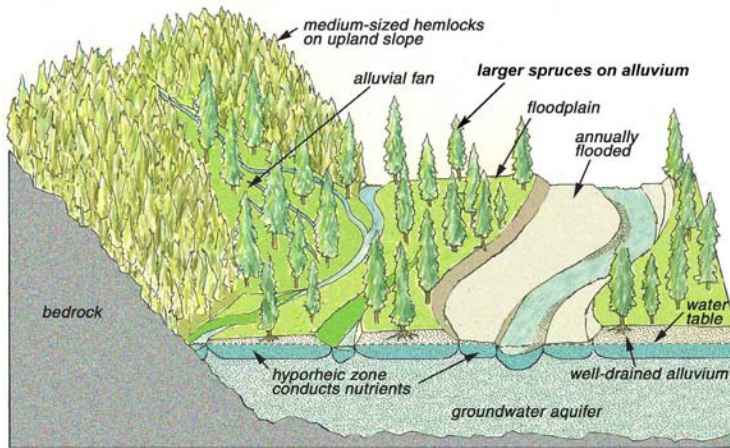
FIG 21 Relationship of large-tree forests to alluvial fans and floodplains. (Slope is exaggerated on alluvial fan.) Average tree diameter is larger on well-drained alluvial soils, and stands are more widely spaced. Understory plants are better lit and nourished, producing more berries.

The hyporheic zone is the saturated sediment beneath streams and rivers where ground and surface water meet. This zone extends far from the wetted channel in some floodplains, transporting salmon- and alder-derived nutrients throughout the alluvium.

the valley bottom or one of the raised marine terraces enveloping the highland core of many Southeast islands—velocity slows and sediment is deposited. The stream migrates back and forth over the fan, eventually building it highest in the center (convex in transverse section). In the active phases of fan construction, the stream often splits and "braids," as if undecided where to go (Fig 20).

A new branch of hydrologic research is delving into the hyporheic zone, the saturated sediment beneath and beside streams and rivers where ground and surface water meet (Fig 21). The rich but scarcely documented microfauna of the hyporheic zone often dominates the biological productivity of rivers. Beneath broad flood plains or fans, the volume of hyporheic habitat may be 2,000 times greater than actual channel volume, yet only recently have the ecological implications been considered (Edwards 1998). (Hyporheic dynamics are discussed under "core community" below.)

Tree growth and species composition on alluvial surfaces—whether on flood plains or fans—are influenced by frequency of flooding disturbances. During the Little Ice Age many alluvial surfaces in northern Southeast were rejuvenated by increased flooding. Most of the Landmark Tree sites (see Landmark Tree Project, pg 15) in northern Southeast are what might be called "young old growth." Dominant trees on these streams are impressively large, but often only 2 or 3 centuries old. In contrast, most Landmark Tree stands in the southern Tongass are ancient forests on more stable alluvium. Hemlock and blueberry are larger components in these stands.

Colluvium

This is simply a fancy term for features more commonly known as rockslides or talus. The value of

the more academic term is in calling attention to the similarities and frequent intergradations between this landform type and alluvium.

Like alluvium, colluvium often builds fan-shaped deposits, but gravity, rather than moving water, is the primary agent. Colluvial fans are steeper than alluvial fans. Boulders and cobbles on colluvial fans lie at the angle of repose. The largest boulders often roll to the bottom, with smaller material at the apex. On alluvial fans, in contrast, the boulders are found at the apex, with particle size decreasing toward the fan toe. This gradation is visible in Figure 20. Both colluvial and alluvial fans are well-drained and receive nutrient inputs from the slopes above in the form of sediment and groundwater. Massive trees can therefore be found on colluvial slopes, but they are generally

FIG 22 Canopy view of alluvial spruce forest along the riparian border of Trout Creek, Kosciusko Island. Salmonberry/devil's club thicket occurs in the canopy gap on lower right. Compare the starry "radiating arm" structure of the spruce branches to the foliage of the hemlock trees in the similar oblique view in Figure 16; the hemlocks give more complete coverage and intercept more snow in winter.

This is the kind of habitat where bears congregate in late summer and fall to fish for spawning salmon.

scattered, with fewer large trees per acre than are typically found on alluvium.

In mountainous landscapes such as northeast Chicagof Island, colluvial fans may merge along the bases of valley walls to form "colluvial aprons." The steeper slopes of colluvial fans are sensitive to disturbance. Loss of forest cover can set up chain reactions of landslides and mass wasting both up- and downslope from the disturbance.

Forest Structure

Figure 23 shows a conceptual profile through an old-growth large-tree forest on alluvium. This 1-acre (0.4-ha) block profile is also the "culmination" of the successional series in Figure 48. It probably takes 400 years or more to develop a stand structure like this. (Note, however, that in the 3-part successional series in the Landmark Trees sidebar, this stage would merely be called "middle age!")

All of the stand dominants in the 1-acre (0.4-ha) block of Figure 23 are spruce. The tallest are about 175 ft (50 m). Hemlocks also reach impressive heights for the species on alluvium; in this example, about 150 ft (46 m). Because trees are more widely spaced than in younger second growth or even in upland hemlock old growth, more of the tall trees have branches and foliage at lower levels; compare this "crown depth" in Figures 15 and 23. Because floods have influenced this forest from its earliest stages (Fig 48), the alluvial forest shown has never experienced a shady, stem-exclusion phase; it has always had a gappy canopy, with abundant light to the lower tree foliage and understory plants. The mature alluvial forest occupies an extreme upper-left position in the size-density matrix for Southeast forests (Fig 11); average diameter is very high, and stand density is very low.

Although the forest in Figure 23 is fully deserving of the term "old growth," it could be carried forward in time for another few millennia and become a "senescent" large-tree forest, the last block diagram in the Landmark Trees sidebar. By this time, hemlock holds more volume than spruce. Only 2 of 75 1-acre (0.4-ha) sites documented by the Landmark Trees Project during 10 field seasons were forests of this antiquity. The original, prelogging extent of this type is unknown, but these forests seem to have been relatively uncommon and restricted to alluvial

FIG 23 Conceptual profile of very old riparian spruce forest. The 1-acre (0.4 ha) block is 208 ft (63 m) on a side. Spruce dominates on the rich, well-drained soils, but after several centuries hemlocks come up through canopy gaps. See also Fig 48 for interpretation of the successional development leading to this stage. Streamsides may also receive important marine nutrients from spawning salmon, redistributed by bears and other wildlife.

platforms near the mouths of down-cutting streams where overbank flooding has not been possible for millennia. The largest-diameter spruces remaining on the Tongass—9–11 ft (2.7–3.4 m)—are found on these ancient alluvial surfaces (and on a few remnant patches of unlogged karst). These forests are multi-generation. The oldest individual trees may approach 1,000 years, but the stand itself is much older.

Understory

The understories as well as canopy structure and tree composition of alluvial forests are distinctive. These unique understories respond to depositional history and water table fluctuations. Parklike stands of Sitka spruce have higher shrub biomass than those of hemlock old-growth (Alaback 1982).

Large canopy gaps promote luxuriant understory that tends more toward devil's club and salmonberry than to the blueberry and menzesia shrubs of upland hemlock-dominated old growth. On very active flood plains, stink currant (*Ribes bracteosum*) also may be abundant.

Devil's club and stink currant (and to some degree salmonberry) are offered in clusters on the stem; they make their fruits available in a concentrated mouthful compared to those of blueberries where single smaller
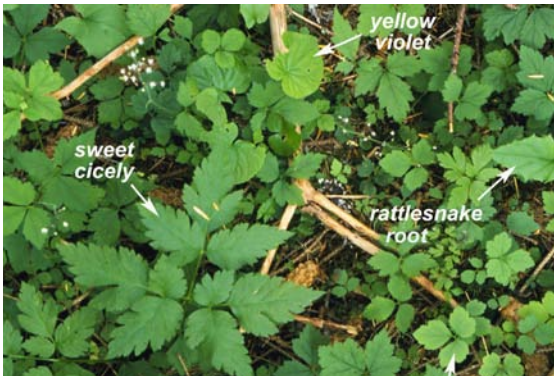
FIG 24 Final product of bear dining on devil's club berries, another high value late summer riparian food.

FIG 25 Stink currant (*Ribes bracteosum*) is one of the berries offered in clusters that bears eat to put on weight prior to fall denning. It's common on active alluvial surfaces with regular flooding disturbance.

FIG 26 Common riparian herbs. Only foamflower (*Tiarella trifoliata*) will remain green in winter. Yellow violet (*Viola glabrescens*), rattlesnake root (*Prenanthes alata*) and sweet cicely (*Osmorhiza purpurea*) provide only summer forage for deer.

bites must be selected. The nutrient-rich and well-lit alluvial understories make it possible for the clustered berries to fruit abundantly year after year; in shadier forests, blueberry may go several years between fruitings (P. Alaback, unpublished data, University of Montana). Riparian berry shrubs have thus coevolved with berry-eating animals that are particularly abundant along streams and who efficiently distributed their seeds throughout the streamside corridor. While songbirds certainly consume these fruits, the most effective seed distributors of these riparian shrubs are probably bears (Willson and Gende in press). Bears drawn to the salmon runs also eat and distribute berry seeds, and of course, deposit scats in the perfect growing environment: rich streamside alluvium.

In studies comparing riparian to upland herbaceous communities, the riparian zone was much more diverse, with 23 unique species compared to only 8 in the upland forest (Alaback and Sidle 1986). Riparian herbs flourish in wet soils close to streams; examples are grasses and sedges, enchanter's nightshade (*Circaea alpina*), violet (*Viola spp.*), and cow parsnip (*Heracleum lanatum*). The moss and liverwort flora in the stream and splash zone is also unique (Alaback and Sidle 1986).

In addition to well-drained alluvium, the slower reaches of streams and intermittent side channels are often rimmed by poorly drained, mucky habitats where dense patches of skunk cabbage (*Lysichiton americanum*) grow. These places are very important for foraging deer and bear.

Typical riparian herbs are shown in Figure 26. With the exception of foamflower, these leaves wilt in the fall. This growth pattern differs from that of upland hemlock forbs like ground dogwood and trailing raspberry that stay green all winter. Consequently, the riparian and upland forests play different seasonal roles in the lives of grazing animals.

Wildlife

Intensive telemetry studies by the ADF&G have been conducted for both deer and brown bear on Admiralty and Chichagof islands. Results show that wintering Sitka deer make little use of riparian spruce forest (Schoen and Kirchhoff 1990). (Quick Cruise sidebar.)

For bear, the results are very different. In 1 study, habitat use data were collected from 95 radio-collared brown bears on Admiralty and Chichagof islands (Schoen and Beier 1990). From mid-July to early September, 54% of collared bear relocations were in riparian spruce/devil's club forest and 66% occurred within 525 ft (160 m) of anadromous salmon streams.

FIG 27 Ancient spruces to 9 ft (2.7 m) in diameter on apex of alluvial fan, southern Admiralty Island, the 4th highest-scoring Landmark Tree site. Note the abundance of devil's club in the understory

In subsequent studies on northeastern Chichagof Island, 63% of 2,069 brown bear relocations were in riparian habitats fringing the 25 key salmon streams (Titus and Beier 1999). Section 6.2 provides more details on brown bear habitat use.

Mink (*Mustela vison*) on Southeast salmon streams appear to have delayed their breeding cycle so that lactation occurs at the time of salmon carcass availability. Fledgling bald eagles (*Haliaeetus leucocephala*) leave the nest as pink salmon (*Oncorhynchus gorbuscha*) return (Willson et al. 1998). Even wildlife not typically thought of as directly dependent on salmon may be more common in riparian forests because of the high value of the salmon-based food chain. Nesting songbird densities were higher on anadromous streams than on similar streams lacking salmon. One of several possible reasons for this nest density is that decomposing salmon promote higher abundance of insect prey for songbirds (Gende and Willson 2001).

"Core Community"

Interdisciplinary research is uncovering relationships between salmon and salmonberries, upwellings and nutrient pulses, and fish carcasses and riparian birds that few suspected a decade ago. These findings reinforce a growing belief that the riparian community of spruce, salmon, bear, eagle, and devil's club is an important foundation of coastal rain-forest fertility. The riparian spruce forest is where the great pulse of marine productivity is returned to the land, and where the land incubates and nurtures salmon and other anadromous fish. Birds, mammals, and fish from every surrounding terrestrial and marine community migrate annually to the riparian large-tree forest to partake of the stream's bounty.

One branch of stream-community research employs isotopic markers to identify marine-derived nutrients returned to the land by spawning salmon. These nutrients end up not only in terrestrial salmon predators and scavengers, but also in riparian vegetation like devil's club and stink currant many yards (m) from the stream. On some streams, bears carry half of the spawners to shore, where the fish either decompose or return to the soil as bear scat, providing nitrogen, phosphorus, carbon, and micronutrients (Willson et al.1998).

Just about everything "eats" salmon, directly or indirectly. Juvenile salmon themselves also benefit indirectly from the disintegrating bodies of their parents, because juveniles eat aquatic invertebrates that feed in turn on the mat of algae, fungi, and bacteria covering fish carcasses (Wipfli et al. 1998).

Limiting nutrients for plants and animals of the riparian forest include nitrogen, phosphorus, and lipids (fat). Nitrogen is contributed by both alder and salmon, and salmon are rich in all 3 of the limiting nutrients. The efficiency with which these alder- and salmon-derived nutrients can be distributed throughout a flood plain is better comprehended when one considers the unseen movement of groundwater in the hyporheic zone (Fig 21). This saturated sediment stores and transports nutrients. Hyporheic upwellings deliver pulses of nitrogen and phosphorus to side-slough algal colonies and to soils far from the channel, sometimes even in spring, months after the salmon runs have ended (Gende et al. 2002).

KARST LARGE-TREE FOREST

Karst refers to a distinctive landscape developing on water-soluble limestone and marble. Unlike alluvium, which is found to some degree in every watershed in Southeast, karst is erratically distributed. Because the large-tree spruce forest on karst is essentially gone, forest ecologists have little direct experience or data to draw from. But some stands of large-tree hemlock and redcedar remain on karst. And where karst was logged, there is potential for slow restoration of this rare and important forest type.

As with the riparian large-tree spruce forest described above, the karst large-tree forest falls within the highest size/density class (SD-67) of Caouette and DeGaynor (2005). The karst large-tree forest was the greatest of the upland (i.e. non-alluvial) forest types. Even the remaining examples have extremely high habitat values, thus deserve special attention in a conservation assessment.

Karst as a Forest Substrate

The rooting environment for trees on carbonate rocks is called "epikarst," the intensely dissolved veneer at the surface of karst formations. Epikarst is usually about 6 ft (2 m) thick at low elevations, and up to 100 ft (30 m) thick in more exposed alpine karst (Baichtal and Swanston 1996).

Karst grows large trees for some of the same reasons alluvium does. The high water tables and surface ponding that limit tree growth on many surfaces in Southeast are uncommon on the fissured, highly permeable karst landforms. Figure 29 compares the glimpses of protruding bedrock in a forest understory to a small, mostly bare karst island. In the latter, it is more obvious that karst is studded with crevices and sinkholes from jacuzzi-sized to micro-cracks. Rainwater flows through these entry points directly into the underground cave system. Surface streams are uncommon in many karst landscapes. On forested karst, tree roots deeply penetrate and grip the dissected carbonate bedrock, providing stability in high winds.

The flora of Southeast is generally tolerant of the acid soils of coniferous forests, but many plants reach optimum growth where this acidity is buffered. Carbonate rocks elevate the pH in soils, groundwater, and streams. The high productivity of lowland karst is also due to rapid carbonate weathering and soil formation (Streveler and Brakel 1993). Karst soils on valley floors and on slopes below 400 ft (120 m) are nutrient rich (Baichtal and Swanston 1996). Resulting in part from the deeper soils and the gentler slopes below 400 ft (122 m), most of the great karst forests once grew at these low elevations.

FIG 28 Sitka spruce on karst, southern Kosciusko Island. This tree measures 9.7 ft (3 m) in diameter and stands 205 ft tall (62.5 m). It scores slightly higher than the official state champion spruce (582.5 versus 555.5 points). Stump measurements suggest that considerably larger trees once grew on karst in southern Southeast.

Forest Structure

It is more difficult to characterize the large-tree spruce forest on karst than on alluvium, partly because so few of the greatest karst forests remain. But the karst forest does seem inherently more variable. Some lowland karst shown in red in Figure 30 supports unremarkable forests. An example is the Angoon Peninsula on Admiralty Island, where low-grade Devonian-aged schistose marble underlies brushy stands of small- to medium-sized hemlocks.

An intermediate example can be seen at 500–1,000 ft (150–300 m) on karst hillsides in the Cholmondeley Sound area on southern Prince of Wales. These slopes support trees of generally modest size throughout which enormous spruces are scattered. Both yellow-cedar and redcedar also prosper on this karst, reaching large sizes for their species.

At the other extreme, on high-quality karst of Sea Otter Sound and Long Island, forests once grew that compared favorably with the great coastal redwood and Douglas-fir stands in the Pacific Northwest—the greatest conifer forests of the world. Trees in northern forests of Southeast reached great age as well as physical dimensions; Sitka spruce can live twice as

long in Alaska as in Washington (Kirk and Franklin 1992). Unlike the alluvial forest that depends upon occasional flooding and initial wide tree spacing to maintain spruce dominance, the karst surface is stable. It is altered only by slow dissolution. In consequence, hemlocks constitute a larger percentage of the stand than in all but the most ancient of alluvial large-tree forests. Because uprooting and soil rejuvenation appears to be uncommon on karst, it is difficult to explain how spruce persist for millennia as a significant stand component on this surface.

Large hemlocks tolerate the shade of the giant spruces, filling in the spaces and resulting in higher tree density than on alluvium. Timber volume is also potentially much higher in the karst large-tree forests. The highest volume for a 1-acre (0.4-ha) alluvial stand measured by the Landmark Trees Project is 140,000 gross board feet per acre (bf/a). The same methods were used in a logged karst "ghost forest" on Heceta Island. Measuring stumps and reconstructing former tree heights from abandoned logs on the forest floor gave an estimated volume of 230,000 bf/a. The largest tree, even after 7 decades of having lost sapwood to rot, measured 10 ft (3 m) in diameter at 10 ft (3 m)

FIG 29 Forested and bare karst surfaces. On left are limey "knees" exposed in understory of handlogged karst on Heceta Island. Vegetation includes sword, maidenhair, and shield ferns (*Polystichum munitum, Adiantum pedatum, Dryopteris expansa*) with stink currant and salmonberry. Photo on right shows surf-exposed karst island at the entrance to Sea Otter Sound.
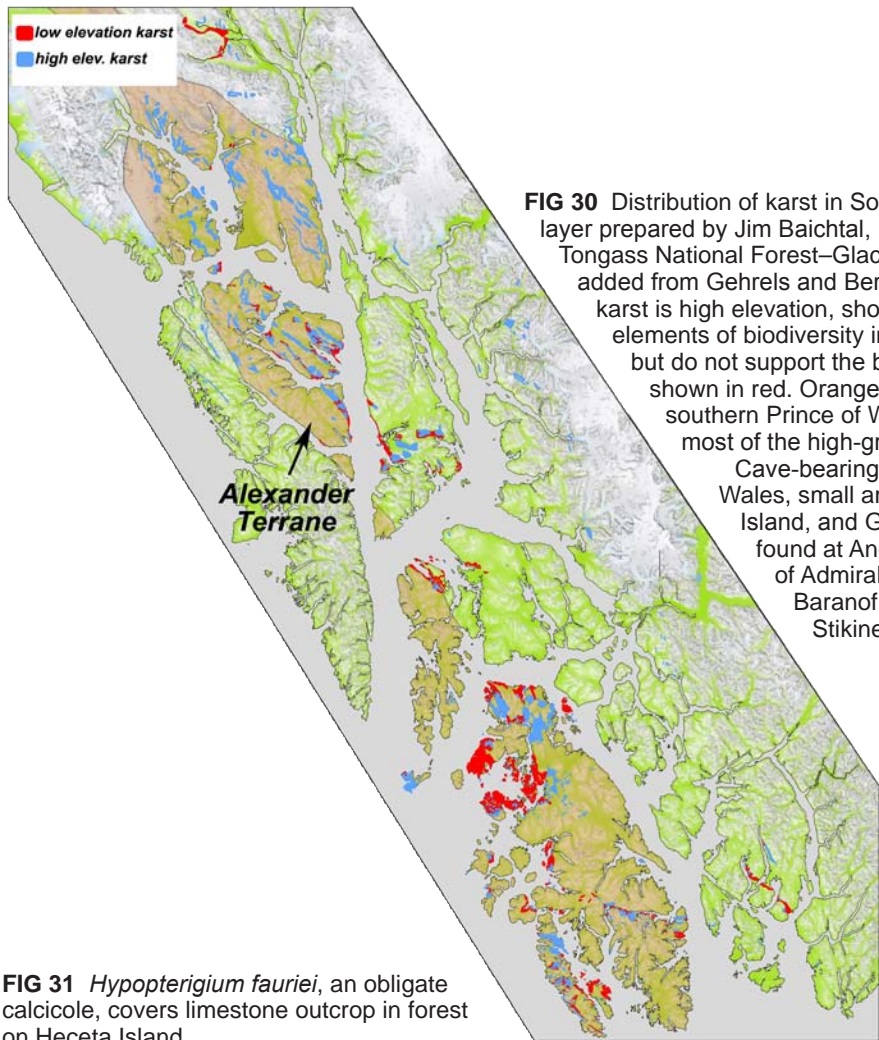
FIG 30 Distribution of karst in Southeast Alaska. Based on original data layer prepared by Jim Baichtal, USFS. Carbonate rocks outside the Tongass National Forest–Glacier Bay and Haines area–have beed added from Gehrels and Berg (1992). The majority of Southeast karst is high elevation, shown here in blue. These are important elements of biodiversity in subalpine and alpine communities but do not support the big-tree forest. Low elevation karst is shown in red. Orange-tinted area running from Glacier Bay to southern Prince of Wales is the Alexander Terrane that hosts most of the high-grade carbonate rock formations. Cave-bearing karst is common on northern Prince of Wales, small areas on Kuiu Island, eastern Chichagof Island, and Glacier Bay. Karst of lesser quality is found at Angoon and in a belt across the highlands of Admiralty Island. It is generally missing from Baranof Island and islands off the mouth of the Stikine River.

FIG 31 *Hypopterigium fauriei*, an obligate calcicole, covers limestone outcrop in forest on Heceta Island.

FIG 32 Green spleenwort (*Asplenium viride*) is a common calcicole on limestone outcrops in the big-tree karst forests of Prince of Wales Island.

above the ground. Root buttresses flared widely below that level; certainly the tree exceeded 15 ft (4.6 m) dbh. These dimensions are much greater than those of the largest living spruce (also on karst) so far discovered by the Landmark Trees Project.

Today's highest-scoring Landmark Tree stand is on carbonate rock near the village of Kake on Kupreanof Island. The largest and second-largest known spruces in Alaska stand 130 ft (40 m) apart on this acre. One is 11 ft (3.4 m) dbh and 225 ft (69 m) tall.

The higher tree density and associated thicker canopies of some karst forests can make them harder to detect on aerial photographs in comparison to gappy alluvial large-tree forests. Alluvial stands are also more predictably arrayed along streams and fans, whereas patches of unmapped karst can appear in any topographic situation. On the other hand, some large-tree karst forests are very gappy.

While the large-tree spruce forest on karst has been almost completely

logged, karst forests of very large western hemlocks and redcedars still remain in places like Prince of Wales. It is currently unknown why some karst once supported giant spruces while other karst supports nearly pure hemlock stands and still other karst substrate supports giant cedars.

Understory

Describing a "typical" understory for the large-tree karst forest is even more speculative than describing the trees and canopy structure. It is hard to know if the few remaining examples are representative of the original forests.

In a study of forest succession, regenerating stands on karst had the lowest understory production of all substrate types because tree growth was greatest and canopy densest (Alaback 1982).

Similarly, in the selectively logged karst forests that rim many of the islands in Sea Otter Sound, understory shrubs and forbs are relatively sparse. The sparse vegetation may have resulted from in-filling

of the originally more complex and gappy canopy. With removal of the giant spruces, the forest canopy became unilayered and interlocking as released and recruiting conifers grew up into the relinquished spaces. Light availability is not the only factor affecting understory plant growth. On the spacious tops of the hand-logged stumps, out of the reach of deer, the ground dogwood and trailing raspberry are more abundant. Herbivory has apparently compounded the problems faced by understory plants in shaded environments.

The understory of the top-scoring karst Landmark Tree stand described above resembles that of shady upland hemlock dominated old growth more closely than that of large-tree alluvial spruce forest. Blueberry covers 30% of the 1-acre (0.4-ha) stand. Cover of deer forbs, however, is much less than 1%.

Contrasting with the sparse understories of these karst forest types is a magnificent stand on southwest Kosciusko Island (Fig 33). Aerial perspectives show this stand to be just as gappy as an alluvial large-tree

FIG 33 Giant spruce on karst, Koscuisko Island. This tree is almost 9 feet (2.7 m) in diameter at 10 feet (3 m) above the ground. (Butt swell makes diameter at breast height–dbh–rather meaningless on such trees.) Surrounding forest is different from alluvial big-tree stands. Ratio of hemlock to spruce is 2:1. Berry plants typical of riparian communities (devil's club, salmonberry and stink currant) are common but so are the winter deer plants of the upland hemlock forest such as blueberry and trailing raspberry. Complex crown structures admit plentiful light.

SOUTHEAST ALASKA CAVES: ARCHIVES OF LIFE IN THE PAST

David Klein

Underlain by limestone bedrock, large portions of Prince of Wales and Dall islands and lesser areas of Chichagof and a few other islands are characterized by numerous caves, sink holes, and disappearing streams. These features of the topography are associated with the numerous solution channels that characteristically develop in the water soluble limestone over the long period that the limestone has been at the surface of the Earth's crust. Exploration and mapping of a large number of caves that occur in the karst topography of Southeast Alaska during the past two decades has disclosed a rich storehouse of fossil material. The high calcium and low acidity of the water that drains through these underground channels and caves provides excellent conditions for bone preservation.

The U.S. Forest Service has attempted to find, map, and explore these caves, which play a unique role in the ecology of the region. Streams flowing through some of these caves provide spawning habitat for salmon and other fish species, some other aquatic species are restricted to the waters of the caves, bats sometimes roost and hibernate in the caves, and Native cultures in the past have made use of some of the caves as shelters and have left petroglyphs and cultural items in the caves. Most importantly, many of the caves contain the bones of animals that have fallen into the sinkholes associated with the caves or, especially in the case of bears, have died while using the caves for hibernation or denning. The caves and the bones they contain and the associated sediments provide an archive of past life in this region of Alaska. Excavations by archeologists and paleontologists have identified bones of animals that occupied the area from the present to more than 40 thousand years ago, indicating that portions of the outer coast of Southeast Alaska were not overridden by glaciers that covered most of the rest of the region during the last glacial period. Brown bears and black bears coexisted there some 9,500 years ago and the record for brown bears goes back more than 30 thousand years. Caribou, foxes and other species now present only on the mainland were also present there.

And bones of a human found in one of the cave excavations date back 9,800 years making them the oldest human remains found in North America to date. This find, and evidence that life for humans there close to the sea was quite possible, has added credence to the hypothesis that the first peoples venturing into the Americas from Asia may have followed a coastal route that enabled them to rapidly disperse throughout the Americas over a relatively short period of time.

The value of the Karst topography of Southeast Alaska includes not only the unique influence it has on the forest ecology it supports on the surface, but it also is a storehouse of information about past life in the area, inclusive of the earliest humans. Unfortunately, the information that that these caves and sinkholes has revealed to date is only a fragment of the potential that exists. Location and mapping of the caves and sink holes of the region has so far only discovered the most obvious ones. Much more remains to be done by the Forest Service. Even with the help of volunteer spelunkers, the Forest Service has not had adequate funding nor commitment to carry out this work. This area of caves and sinkholes ranks with Mammoth Cave in Missouri and Carlsbad Caverns in New Mexico, both part of the National Park system. Identification and mapping of all existing caves and sinkholes in the region must be completed prior to planning for any surface activities, such as road building, logging, and other development activities that can block entrances and alter drainage systems, threatening the future of these caves.

FIG 34 Cavern Lake, Prince of Wales Island

forest. Walking through this forest is a delightful experience; brushy understory alternates with open mossy areas in an intricate mosaic. Salmonberry is the most common shrub, but other shrubs include stink currant patches in swales and blueberry on small karst knolls. For deer, this forest has the best of both lush summer forage and evergreen winter foods.

Plants that show a clear preference for lime-rich rocks are called "calcicoles" (Kruckeberg 2002). Calcicoles give a distinctive appearance to many karst forest understories. Among vascular species there are few obligate forest calcicoles, but many seem to do especially well on carbonate rocks. (Regional Variation in Section 5.3 gives examples of obligate calcicoles at alpine elevations.) Sword fern and maidenhair fern are particularly abundant forest calcicoles (Fig 29). More easily overlooked are the small spleenworts (*Asplenium viride* and *trichomanes*) that hang from limey outcrops. Among mosses, obligate calcicoles may be more common; the species *Hypopterigium fauriei* (Fig 31) has only been found on carbonate rocks (E. Anderson, Botanist, [USFS] Juneau Ranger District, Juneau, AK, personal communication 1999).

Wildlife

Studies of fish streams on karst have shown that rearing coho (*Oncorhyncus kisutch*) reach greater sizes and densities than in comparable non-carbonate streams (Bryant et al. 1998). Virtually nothing is known about the big-tree karst forest as habitat for birds and mammals. Because of the small size of remaining large-tree spruce karst forests, wildlife research opportunities are very limited.

Deer forage plants growing on carbonate rock may contain higher calcium levels, allowing for better bone and antler development (Baichtal and Swanston 1996). It is common knowledge among hunters that the largest bucks with most massive antlers come from the limestone country of Prince of Wales Island; however, data on relative weights for deer on differing bedrock types are not available.

In addition to the widespread little brown bat (*Myotis luicifugus*), several species with limited records in Southeast roost in limestone caves during the period of winter torpor. California myotis (*M. californicus*), long-legged myotis (*M. volans*), and

silver-haired bat (*Lasionycteris noctivagans*) all have probable karst associations (USFS 1997).

CEDAR/HEMLOCK

Western redcedar (*Thuja plicata*) and yellow-cedar (*Cupressus nootkatensis*, formerly genus *Chamaecyparis*) both belong to the cypress family of conifers. (Neither species is a true cedar; thus the odd spellings. Yellow-cedar is hyphenated, as in "Douglas-fir.") Because the Western redcedar and yellow-cedar share certain habitat affinities, they are considered together here. Both species grow as dispersed individuals in a variety of habitat types, including the wet, small-tree forest described later in this chapter.

Neither species of cedar commonly occurs in pure stands, but each can be important or even dominant components of their communities (Fig 35). Because western hemlock is almost always an associate, such forests are commonly referred to as "cedar/hemlock." or "hemlock/cedar". Tables 1 and 2 compare the cedar/hemlock forest as described in this report with other existing USFS forest classifications. As with the upland hemlock forest, cedar forest types described herein span the full range from low to high productivity.

It's difficult to map the distribution of the red- or yellow-cedar forest. In that regard, the cedar forest is an exception to this report's general emphasis on forest types that are accurately captured by existing GIS layers. Cedar mapping is clearly a major data gap. Similarly, no studies of the ecology or wildlife habitat values of cedar forests have been conducted in Southeast.

In Alaska, both cedar species are able to tolerate harsh sites with less competition from other tree species. Their strategy is in high allocation towards defense (allelochemicals), permitting great longevity. With their minimal nutrient requirements and slow growth rate they can dominate on fairly stable moist sites.

In Washington and Oregon there are some exceptions to the harsh site rule; redcedar there once grew to enormous size (>20 ft [6 m] diameter) on rich alluvial bottomlands. In Southeast, at the northern limit of its range, redcedar occurs mainly on wet to boggy sites (Pojar and MacKinnon 1994). On a few

FIG 35 Exceptionally large redcedar on the beach fringe, Chasina timber sale area, Prince of Wales Island.

FIG 36 In the Pacific Northwest yellow-cedar is strictly a mountain tree. Northward up the coast its elevational range declines. In southern Southeast it tends to be replaced by redcedar at elevations below 500 to 1,000 feet (152-305 m). Yellow-cedar range from Arno (1984). Redcedar elevational limits from Pojar and MacKinnon (1995) and Farrar (1995).
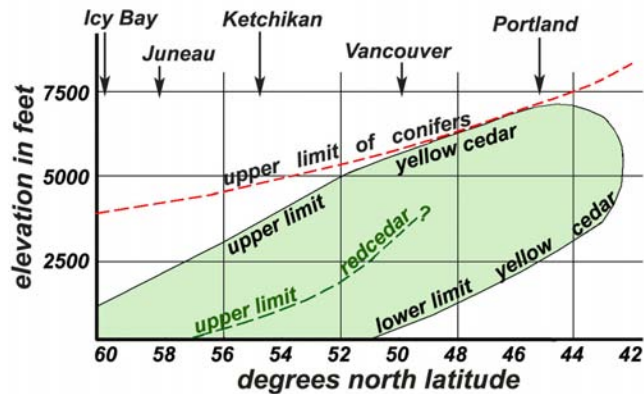
highly productive sites such as karst hillsides, very large western redcedars may be found in Southeast. The state record redcedar is 9.5 ft (2.9 m) diameter at breast height (dbh)—the same diameter as the official state record Sitka spruce. (Redcedar is shorter than spruce, however.)

At low elevation in southern Southeast, redcedar out-competes yellow-cedar. Higher on upland slopes, the more snow-tolerant yellow-cedar replaces redcedar, often abruptly (Fig 36). In the Ketchikan area, yellow-cedar reaches greatest abundance at about 1,000 ft (305 m) in elevation.

Both cedar species are relatively short trees with massive bases in old age. They taper to spindly, often-dead tops with drooping foliage. These features make yellow-cedar and redcedar the most windfirm of the Southeast conifers (Harris 1989). Volatile oils in the scale-like leaves inhibit insect herbivory. In the Rockies and Coast Ranges, western redcedar commonly lives 1000 to 1500 years, and a yellow-cedar in British Columbia lived over 2000 years. Heart rot makes aging of yellow-cedar difficult after about 700 years, but the species is clearly the most venerable of Alaskan trees (Hennon and Shaw 1997).

Yellow-cedar extends from northern California to Prince William Sound. In the Cascade Ranges this species is a timberline tree occupying marginal habitats with short growing seasons (Arno 1984). At the latitude of Vancouver (Fig 36), yellow-cedar can be found at sea level, but in these lower elevations it is out-competed by other conifers on productive sites and is found primarily on poorly drained soils as a member of the small-tree forest. In Southeast, yellow-cedar has a spotty distribution and is absent from many apparently suitable habitats. On Chichagof and Baranof islands, yellow-cedar is present throughout a soil-drainage gradient from open bog to drier, more productive sites; however, it is the dominant conifer by basal area on transitional sites with intermediate drainage (Hennon 1992).

Because pollen of this genus does not endure as long in peat samples as that of other conifers, yellow-cedar has been overlooked in studies that used radiocarbon dating to determine colonization history. Foresters do not know if the current scattered "islands" of yellow-cedar reflect contraction from a previously more continuous range or if the species has recently expanded into these areas. There is some indication that yellow-cedar may have survived the Wisconsin Glaciation in coastal refugia near today's Dall Island (P. Hennon, Forest Pathologist, Forestry Sciences Laboratory, Juneau. personal communication, 2006)

Western redcedar seeds more prolifically and is more shade-tolerant than yellow-cedar, possibly explaining its greater abundance in relatively

productive forest sites where spruce and hemlock grow tall enough to cast shade on cedars.

Although the cedars are well defended against insects, both are heavily browsed by deer as seedlings and saplings, inhibiting reproduction. A puzzling lack of yellow-cedar seedlings and saplings in some clearcuts may be due in part to deer browsing. Warmer winters with light snow cover allow deer access to young clearcuts. Therefore, global warming may lead to heavier browsing. Some foresters speculate that during the recent Little Ice Age, deer populations reduced by deeper snows allowed better seedling survival and subsequent range expansion of yellow-cedar (Hennon 1992).

But deer browsing is not the only factor in poor reproduction by yellow-cedar; seedling survival seems poor even on islands like Kuiu that have low deer populations. Foresters have experimented with planted cuttings (stecklings) and noted excellent survival (Hennon and Shaw 1997). However, planting is not a viable solution to poor reproduction of yellow-cedar across its range.

Western redcedar is more sensitive to cold and snow than is yellow-cedar. In severe winters, redcedars at their northern range limits may suffer snow breakage of leaders and limbs. Pollen records indicate that western redcedar has expanded northward up the Pacific Coast following deglaciation and warming climates. It first appeared in northern Washington about 6,000 years before present (BP). Redcedar reached Prince Rupert at the southern border of Alaska only 2,500 years BP, and did not colonize the Queen Charlotte Islands until the last millennium (Hebda and Mathewes 1984). Old redcedars on the Haida Gwaii and Prince of Wales Islands may be the first generation of their species on these sites.

Redcedar was the most important conifer for all of the coastal tribes, used for fiber, house construction, and the canoes that endowed these cultures with a mobility unavailable to other Native groups.

Yellow-cedar Decline

The same warming climate that appears to be fostering northward expansion by western redcedar may be at the root of a mysterious and widespread decline of yellow-cedar. More than 500,000 acres (200,000 ha) of yellow-cedar forest have died since the 1880s in Southeast. This forest loss is the most severe decline documented in western North America (Hennon and Shaw 1997) (Fig 39).

Yellow-cedar wood is extremely durable, and the slender dead tops of these trees remain intact for many decades after the tops of spruce and hemlock

FIG 37 Slender dead tops signal dieback of decay-resistant yellow-cedar in Reid Bay, Kuiu Island. Dead wood of other conifer species rots sooner, resulting in thicker, broken-off tops.

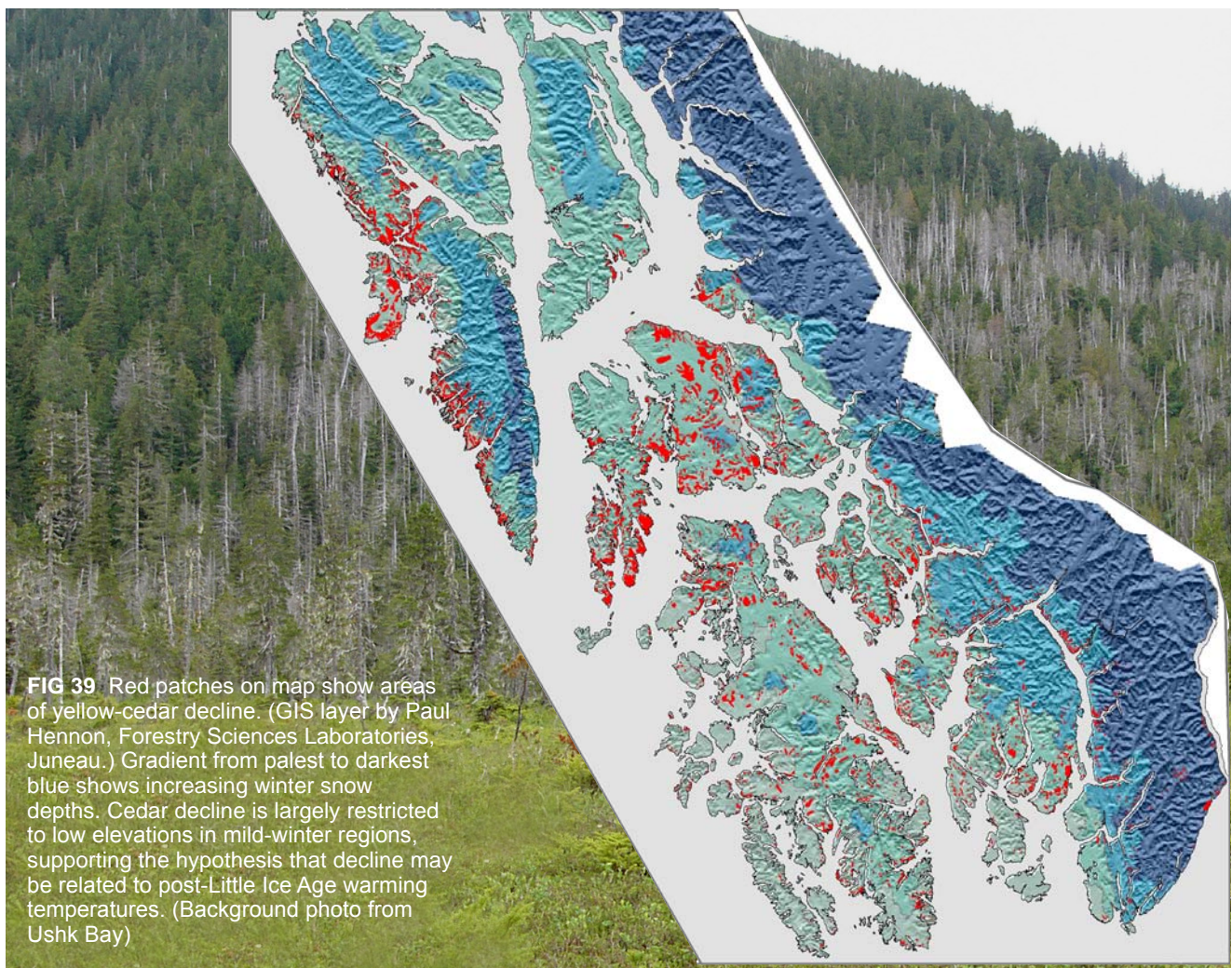**FIG 38** Ancient yellow-cedar, Ushk Bay, Peril Strait.

snags fall off. Dense snag patches are therefore easily recognizable from the water (Figs 37 and 39) and the air. Historical sequences in aerial photographs beginning with early U.S. Navy shots in 1929 suggest few new dieback patches have developed since the onset of decline about a century ago; instead, dieback moves slowly outward from the original patch borders. Mortality occurs mostly at low elevation on wet, poorly drained soils in open-canopied stands.

Researchers at the Forestry Sciences Laboratories in Juneau have intensively studied yellow-cedar decline and determined that it is probably not caused by a biological agent. The decline seems instead to be climate-related. Weather records extend back only to the early 1900s, whereas the onset of decline dates to the 1880s. Glacial recession accelerated at about that time, indicating a sudden warming. Milder winters with shallower snow accumulation may be exposing root systems to freezing on a more regular basis. Fine root necrosis is one of the initial symptoms of dying cedars (Hennon and Shaw 1997).

Bright-yellow, aromatic heart wood; narrow grain; and extreme decay resistance make yellow-cedar the most valuable wood per board foot in Alaska. Almost all of it is exported to Japan, where it is a revered replacement for the vanishing native hinoki (also a *Chamaecyparis*). Like western redcedar, yellow-cedar has many uses in native culture such as totem poles, dishes, and bark fiber for weaving. Trees continue to be stripped for bark near Native communities. Yellow-cedar smoke from wood stoves is the signature aroma of many Southeast villages in winter. In addition to these utilitarian values, ancient yellow-cedars hold records of a millennium of changing climate in their annual rings (Hennon 1992).

FIG 39 Red patches on map show areas of yellow-cedar decline. (GIS layer by Paul Hennon, Forestry Sciences Laboratories, Juneau.) Gradient from palest to darkest blue shows increasing winter snow depths. Cedar decline is largely restricted to low elevations in mild-winter regions, supporting the hypothesis that decline may be related to post-Little Ice Age warming temperatures. (Background photo from Ushk Bay)

Succession on Well-Drained, Low-Elevation Habitat

The stages below cover a successional series on well-drained lowland soils from the earliest herbaceous colonizers to the old-growth forest types described previously. This community development can take many alternative pathways. At each successional stage some of the most important habitats for fish and wildlife are noted.

HERBACEOUS COMMUNITIES

Only the most violent of disturbances can knock a forest community all the way back to herbaceous successional stages.* More typically, as with logging or blowdown, the initial response to disturbance is dominated by shrubs and tree saplings (Fig 40).

In Southeast, *wet* herbaceous communities are abundant; however, meadows on *well-drained* surfaces are fairly uncommon and usually ephemeral, because forest will be the ultimate habitat there. One such community—the uplift meadow on surfaces raised from tidal elevations by glacial rebound—is described in Chapter 5.3. Another high-mountain meadow community type is discussed under Subalpine Parkland Subzone. Evidence indicates that with global warming even the subalpine meadows are slowly succeeding to shrub and eventually forest stages, but rates of change there are much slower than at sea level (Lawrence 1958).

A third type of meadow community that can be maintained in early-successional status indefinitely by repeated disturbance occurs in fairly small patches or linear strips on the slopes of very active avalanche chutes. These sites are swept so frequently

FIG 40 Secondary succession after logging. Four-year-old clearcut near Point Baker, Prince of Wales Island. Most of the small conifers are spruces that seeded in on the heavily disturbed soils. Slash on this site is mostly fragments from ancient, hollow-centered hemlocks that fell apart during logging.
The much greater quantity of soil and debris here will result in more rapid forest growth and quicker canopy closure than in the deglaciating landscape below.

FIG 41 Primary succession after glacial retreat. Dwarf fireweed and willow colonizes bare schist bedrock with sparse till veneer near the receding terminus of the Mendenhall Glacier near Juneau. Compare the successional profile for post-glacial development (Fig 49) with the profile for post-logging succession (Fig 47) .

*Fire can do this but it is very rare in the northern temperate rainforest (Figure 52 shows exceptions in northern Lynn Canal). This makes our forest quite different from Douglas fir stands of western Oregon and Washington, In Southeast, wind is the dominant natural disturbance and it is less conducive to the creation of young herbaceous communities.
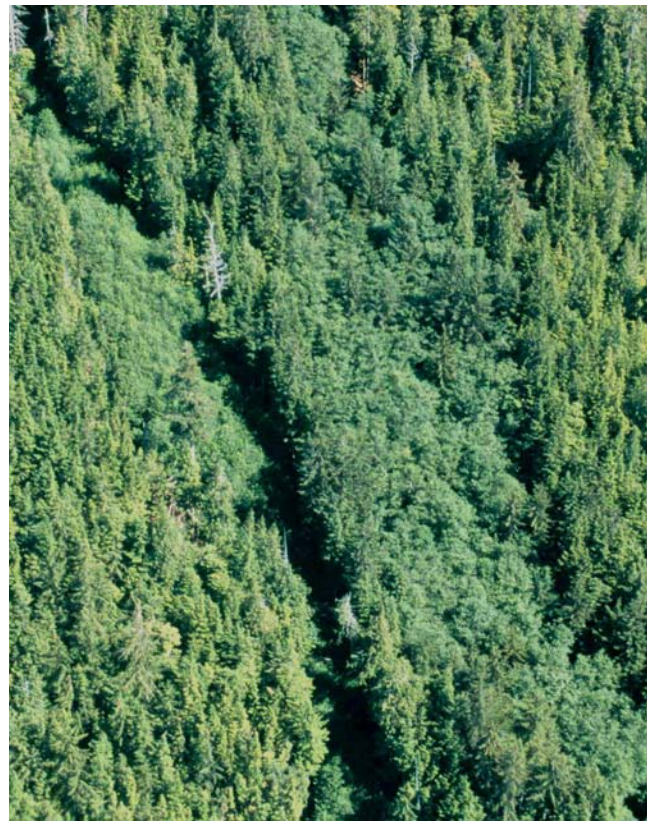
FIG 42 Mature Sitka alder thicket. The Mendenhall Glacier uncovered this site 60 years prior to the photo (stage C in Fig 49). In many places this successional stage can only be traversed on hands and knees.

FIG 43 Sitka alder in steep slide chute framed by hemlock/cedar forest, Gravina Island. These habitats are almost never entered by humans and offer secure cover as well as forage for deer and bear.

that even the flexible Sitka alder (*Alnus crispa*) is incapable of gaining a foothold. Instead, productive communities of grasses, sedges, ferns, and tall herbs like fireweed (*Epilobium angustifolium*) and cow parsnip (*Heracleum lanatum*) may develop, growing most luxuriantly on colluvial toe slopes. These plants are relatively immune to snow and rock fall because they die back to their root systems in autumn, allowing slides to sweep harmlessly over them. As with other lush meadow types, the slide-chute meadows are favored by grazing deer and bear. If the slope faces southward, it will melt free long before the surrounding habitats. Mountain goats (*Oreamnos americanus*) make extensive use of these slide zones, sometimes descending to unmountainously low elevations, especially during spring green-up.

At the snouts of receding glaciers throughout the Southeast mainland, wind-distributed plants colonize surfaces essentially devoid of organic material, resulting in a more spartan herbaceous community scarcely deserving of the term "meadow" (Fig 41).

The process is called primary succession. In its purest manifestation, primary succession is so globally rare that ecologists come to places like Glacier Bay from all over the world to see and study it. (Figure 20 in the preceding section on riparian forests shows raw till and alluvial surfaces in upper Glacier Bay.)

Succession on post-glacial surfaces may take multiple pathways, depending on surface condition and seed source (Fastie 1995). In upper Glacier Bay, the nearest spruce and alder may be many miles away. These species have winged seeds poorly suited for traveling to the bay head from the distant parent plants. There, the first vascular plant to cover the raw glacial till is the plume-seeded yellow mountain avens (*Dryas drummondii*). This mat-forming, rose-family plant is a calcicole that responds to the substantial carbonate component in the Glacier Bay till. Where carbonate rocks are uncommon, as in Mendenhall valley, mountain avens is replaced by species like dwarf fireweed (Fig 41).

In the thin to non-existent soils of primary

FIG 44 Mixed cottonwood/spruce on Drake Island, Glacier Bay (late phases of stage D in Figure 49). Deglaciated 150 years ago. In primary, post-glacial succession, replacement of mixed forest by purely coniferous stands (stage E) can take up to 10 times longer than in secondary, post-logging succession. This also prolongs the tenure of good habitat for species like moose and songbirds.

FIG 45 Mixed aspen and white spruce on Tatshenshini River, BC. This is the boreal version of our alluvial conifer/deciduous forest. Farther downriver in the coastal bioregion, below the Alsek confluence, these cold-winter trees are replaced by black cottonwood and Sitka spruce.

succession, post-glacial dwarf fireweed (*Epilobium latifolium*) or mountain-avens communities rarely achieve the lushness of coastal or subalpine meadows before they are replaced by shrubs and tree saplings.

SHRUB THICKETS

The early shrub stages of post-logging succession on upland sites are dominated by the species that already existed in the understory of the logged forest:

blueberry, salmonberry, and ferns. These species, plus trailing black currant (*Ribes laxiflora*), account for 90% of plant production in young Southeast clearcuts (Alaback 1982). This production increases linearly with time, until the new forest closes canopy after 20–30 years (Harris and Farr 1974, Wallmo and Schoen 1980, Alaback 1982).

Although berry production can be high in the early brush stages of young clearcuts, there appears to be considerable difference for bears between the cutover land and the natural thicket communities of slide chutes (Fig 43) and the open riparian margins that traditionally constitute the major late-summer and fall foraging areas. In a study of radio-collared brown bears on Chichagof Island, only 2.8% of 854 telemetry relocations were in clearcuts (Schoen et al. 1994). Continuing Chichagof brown bear studies
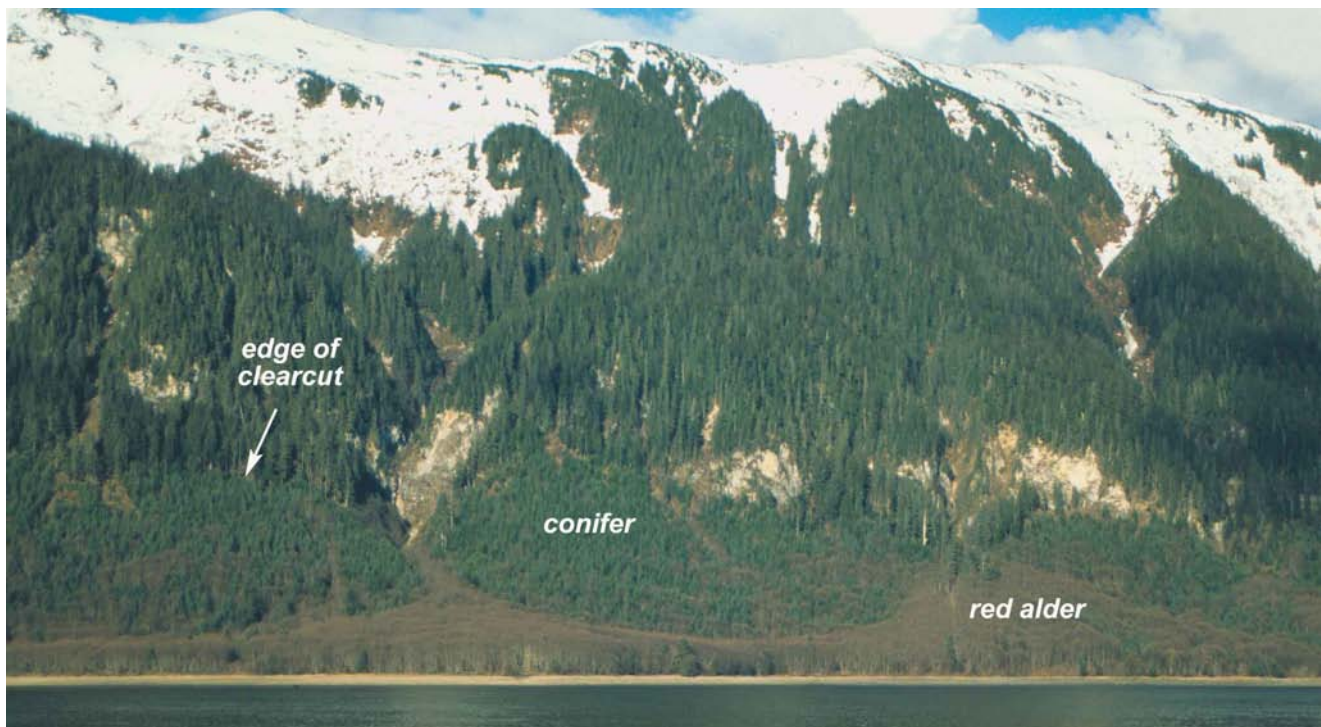
FIG 46 April photo in Tenakee Inlet. Red alder has colonized clearcuts where large spruces once grew on alluvial and colluvial fans in the 1960s and 1970s. On the more gently sloping alluvial fans, trees were removed by tractor-yarding that scarred the soil and encouraged "capture" by red alder. Although foresters have since learned to discourage this alder invasion by using less disruptive yarding methods, some ecologists point out that wildlife values are far higher in mature red alder stands than in equivalent-aged dense coniferous second growth that shades out most understory plants.

further corroborate the findings that brown bears avoid young clearcut habitats (Titus and Beier 1994; R. Flynn, Wildlife Biologist, ADF&G, Juneau, AK, personal communication 2005).

In post-glacial succession, no remnant shrubs from previous communities are poised to inherit the newly uncovered landscape. The first shrub to dominate the landscape is usually Sitka alder. Because its winged seeds do not carry so far on wind as the plumed seeds of willow bushes, the latter dominate thickets in some parts of upper Glacier Bay where the nearest potential parent alders are far down-bay. But on most post-glacial and other early successional surfaces willow (especially *Salix sitchensis, barclayi,* and *alaxensis*) mixes with alder. The mix provides better habitat than could either species alone. Willow is the winter food of choice for beaver, moose, and snowshoe hare (*Lepus americanus*). Alder is less palatable to vertebrates, but produces a nitrogen-rich leaf litter (Crocker and Major 1955).

Soil nitrogen increases very rapidly during the alder stage. Above-ground biomass builds as spruce replaces alder, accompanied by a decline in nitrogen

between 100 and 160 years. The post-glacial biomass of a spruce forest peaks at 120 tons per acre (300 tons per ha) at 110 years. This biomass almost equals the world average for temperate coniferous forests, "quite remarkable given the initial soil conditions devoid of organic matter and nitrogen" (Bormann and Sidle 1990)

Rapid but transient contribution of nitrogen to early postglacial soils affects not only the terrestrial communities that follow alder thickets (Reiners et al. 1971, Lawrence 1979, Chapin et al. 1994), but also streams (Milner 1994) and lakes (Engstrom et al. 2000). In a 2005 Science Integration Workshop at the Fourth Glacier Bay Science Symposium, terrestrial and freshwater ecologists independently concluded that presence or absence of alder in the successional sequence was a fundamental driver of many other trophic and developmental processes in both land and aquatic environments.

Unlike red alder (*Alnus rubra*), which has a single main trunk and grows to 50 ft (15 m) tall, Sitka alder is a multi-stemmed, glorified bush that rarely exceeds 15 ft (4.5 m) in height (Fig 42). The stems are so

FIG 47 Succession after logging on moderately well-drained upland surface (till-mantled bedrock). Block diagrams represent 1 acre, about 200 ft (60 m) on a side; a 100-foot (30 m) tree is half as tall as the block is wide. Spruces are pale blue-green; hemlocks darker green.
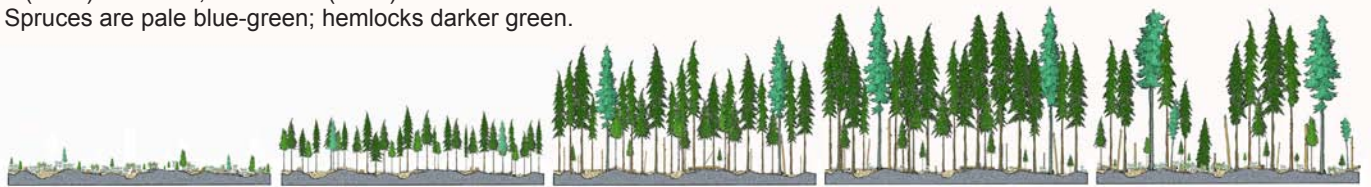
A) A few years after logging. Rapid growth of blueberry and strong release of pre-existing hemlock saplings. Spruces seed-in on soil exposed by uprooted trees.

B) Hemlocks and a few spruces close canopy, killing the understory shrubs and forbs with deep shade.

C) Toward the end of the stand's first century, most of the down wood has rotted. Understory is still shady and depauperate.

D) Gradually the shrub and forb layers return. Subcanopy hemlocks grow very slowly. Spruces, though few in number, are the tallest trees in the overstory.

E) After 3 or 4 centuries mortality produces gappy old-growth mosaic. Abundant deer forage; standing and down dead wood for cavity nesters; decomposing fungi and invertebrates.

FIG 48 Succession on alluvium after a stand-replacing flood. Overbank floods continue to sweep the forest swales until stage D.

Note that forest structure begins to converge by stage E in Figs 48 and 49. Tree growth continues to be more vigorous on alluvium, along with a higher percent of spruce. But both forest types are now "gappy" with abundant dead wood and diverse understory.
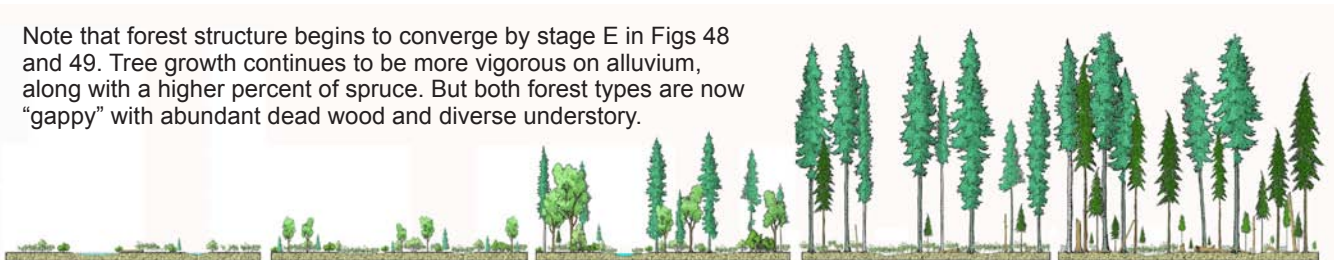
A) Channels still braid through the active alluvium. On higher microsites, cottonwood, willow, Sitka alder (darkest green) and occasional spruce take hold.

B) A temporary reprieve from flooding allows devil's club, salmonberry and stink current to blanket the site. Cottonwoods shoot up at 3 feet per year.

C) Overflow channels reactivated but forest thrives. Spruces overtake cottonwoods but are widely spaced from competition with shrubs and willows in earlier life. This forest never experiences the closed-canopy, depauperate understory stages of the upland series shown above.

D) Sitka spruces on alluvial sites can grow 200 ft (60 m) in 200 years. Shade-intolerant cottonwood, alder and willow have largely disappeared, but an almost continuous thicket of berry bushes remains.

E) River incision has isolated the ancient, multi-generational forest from further flooding. Flood-intolerant blueberry and hemlock arrive. Logging has reduced stages D and E to a fraction of their former extent in Southeast Alaska.

tough and rubbery that they are nearly impossible to break. This stem hardiness allows the entire plant to lie flat under deep winter snow, yet spring up again when the snow melts away. Sitka alder thicket is the community best able to take advantage of conditions that exclude (briefly or perennially) its taller-growing but more breakable competition. Such habitats include the very deep-snow environments near glacier faces and in subalpine bowls. In slide chutes, downward-angling branches of Sitka alder offer little resistance to avalanches of rock or snow (Fig 43).

Other woody-stemmed species of shorter stature are associated with the alder/willow thickets, further increasing the habitat values for fruit-eating mammals and birds. Red elderberry (*Sambucus racemosa*), salmonberry, devil's club, and stink currant are all favored berry plants for bears and post-nesting songbirds like Stellar's jays (*Cyanocitta stelleri*) and varied thrushes (*Ixorius naevius*). After bears leave the salmon streams in late summer, many concentrate on carbohydrate-loading in the berry patches to put on fat for winter dormancy. The slide chutes with their abundant stink currants are key brown bear habitats at this time of year (Schoen et al. 1994).

Sitka alder may also form thickets along streams and roadsides and in clearcuts. In these locations,

FIG 49 Cartoon of postglacial succession in Mendenhall Valley. This is but one developmental pathway, infered from a chronosequence of communities on mesic surfaces below Mendenhall Glacier. Succession on poorly- or excessively-drained surfaces is quite different. (See Fastie [1995] for cautions about the chronosequence approach to successional studies.)

    A. Postglacial barrens with lichens, moss and dwarf fireweed   B. Alder/willow thicket with small spruce saplings. C. Thickets still productive but overtopped by cottonwood and spruce. D. Cottonwood and spruce close canopy over senescing thickets. E. Spruces overtop senescing cottonwoods. Small shade-tolerant hemlocks in subcanopy. Depauperate, moss dominated understory. Only after about 200 years does blueberry become fairly abundant.   F. After many centuries without stand-replacing disturbance, hemlock-dominated old growth develops. This stage is distinguished from "E" by gappy canopy, rich, patchwork of shrub and subcanopy layers, plentiful deer forbs and abundant standing and down dead wood.

    Compare this sequence to post-logging and riparian succession in Figs 47 and 48.
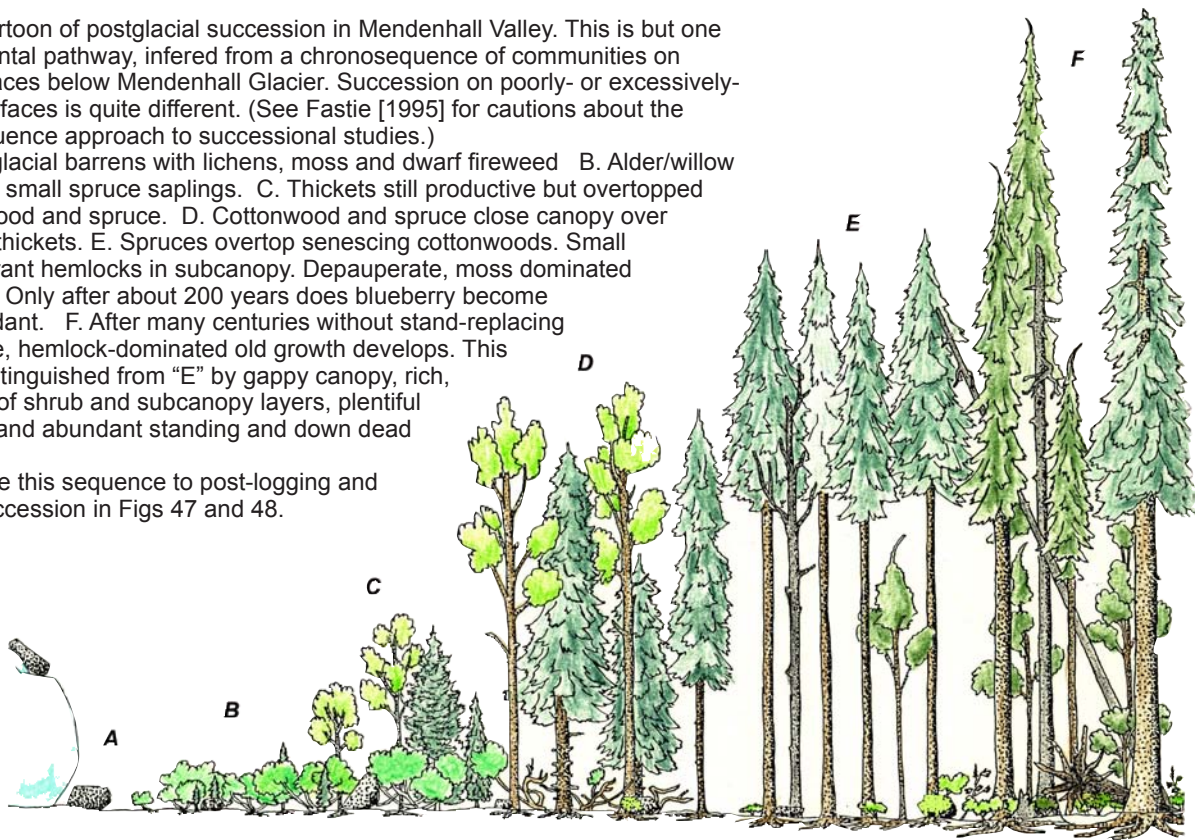
however, where snow burial or avalanche is less intense than in deglaciating landscapes or slide zones, the tree-sized red alder may do equally well or better (Figs 46 and 51).

MIXED CONIFER/DECIDUOUS

Thicket species are short-lived, as indicated in the transition from stages C to D on Fig 49. Because alder and willow are shade-intolerant, young plants rarely survive under the foliage of their parents. Aging willow and Sitka alder bushes begin to die back when overtopped by red alder, black cottonwood (*Populus trichocarpa*), Sitka spruce, lodgepole pine (*Pinus contorta*), or western hemlock. Only in perennially disturbed sites like slide chutes can alder/willow thickets persist indefinitely (Fig 43).

    But if there is a strong deciduous component to the overtopping trees, high fish and wildlife habitat values may endure or even improve for several decades. Only when a uniform conifer forest (Fig 49, stage E; Fig 47, stage B,) closes over the deciduous brush does an impoverished understory of low wildlife value ensue (Wallmo and Schoen 1980, Alaback 1982, Schoen et al. 1988).

Figure 49 shows one of many possible successional trajectories on moderately well-drained, post-glacial surfaces in Southeast. Stages C and D, the mixed conifer/deciduous communities, may persist for more than a century after deglaciation, as on Drake Island (Fig 44), or in active riparian habitats (Fig 48, stages B and C). In contrast, this mixed conifer/deciduous stage may not occur at all in post-logging or post-blowdown succession (Fig 47).

    Large expanses of the mixed conifer/deciduous forest are limited mostly to post-glacial and active alluvial surfaces of the mainland. This rich habitat comprises far less acreage than the purely coniferous rainforest that dominates much of the Southeast forest land. Its sparse distribution may explain the regional rarity of some bird species such as downy woodpecker (*Picoides pubescens*), Hammond's flycatcher (*Empidonax hammondii*), western wood pewee, red-eyed and warbling vireos (*Vireo olivaceus* and *V. gilvus*), Tennessee warbler (*Vermivora peregrina*), MacGillivray's warbler (*Oporornis tolmiei*), northern waterthrush (*Seiurus noveboracensis*), American redstart (*Setophaga ruticilla*), and western tanager (*Piranga*

FIG 50 Selected landcover types on Taku River. On this very active floodplain, cottonwood forest occupies more acreage than spruce. Hemlock forest is restricted to upland slopes above the flood plain.
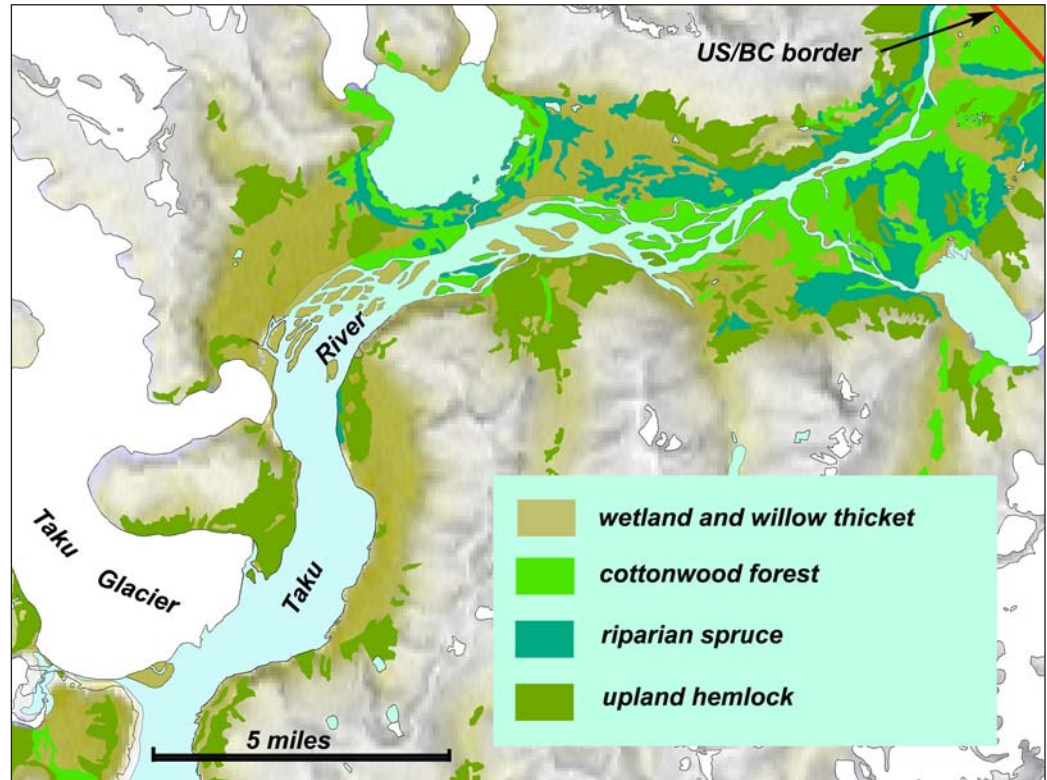
FIG 51 Post-logging succession, Traitor's Cove, Revillagigedo Island. Hemlock/spruce second growth on moderate upland slope. Band of mature red alder in center on frequently scoured channel of intermittent stream. Exposed mineral surface in this channel gave the advantage to alder.

ludoviciana). In evaluating distributions of these species, it can be difficult to differentiate between the habitat affiliations of a bird and the "corridor effect" of lowland passages between Southeast and interior British Columbia where these birds are more common (Gibson and McDonald 1975). Many of these deciduous bird species clearly are found in places distant from transboundary corridors, such as Glacier Bay and Mendenhall Valley (M. Willson, Ecologist, Juneau, AK, personal communication 2005).

In addition to sheltering rare birds, the mixed forest may also offer superior habitat for a wide range

of common Southeast warblers, thrushes, and kinglets (Willson and Nichols 1997). During June kayaking trips from postglacial barrens to mature even-aged spruce forest in Glacier Bay, the intensity and diversity of bird song have been observed to usually peak in the mixed forest stages (Fig 44).

The mixed conifer/deciduous forest stage reaches its greatest extent on the alluvial flood plains of great transboundary rivers in Southeast (Figs 45 & 50, Fig 48, stage C). In these broad, active valley bottoms, summer floods often reach out laterally great distances from the main channels. Where this happens annually or even at decadal intervals, conifers are inhibited. Black cottonwood, however, is supremely well adapted to seasonal burial in fresh layers of alluvium, and can send out new root layers as much as 6 ft (2 m) above the surface on which it originally sprouted.

On the highest, best-drained microsites, spruce gradually gains a foothold on the alluvium. But it often remains widely dispersed, even after the deciduous trees and shrubs have died back (Fig 48, stage D). Meanwhile, an intricate mix of spruce, cottonwood, red alder, and the taller willows provides not only structural heterogeneity, but also a diversity of forage for herbivores and a wide range of niches for insectivores. The scattered coniferous trees begin

FIG 52 Scar from a forest fire in 1999 on the eastern wall of Dyea valley, near Skagway. Pale granite bedrock was exposed when the fire burned away even the organic duff of the previous forest.

That forest itself was recovering from a more extensive burn in about 1890 that extended upslope to the dotted line. Pale green foliage in this August 2005 photo is paper birch. Other forest species are Sitka spruce, western hemlock, lodgepole pine, red alder, and several willows. This forest may eventually succeed to an even-aged spruce/hemlock type with impoverished understory. But forests have burned frequently here, at least since the late 1880s when Europeans began to accidentally set them, so it's unlikely true old-growth will develop. See also Fig 58 for an older post-fire forest near Angoon.

to offer winter cover for creatures such as red squirrel (*Tamiasciurus hudsonicus*), porcupine (*Erithizon dorsatum*), dark-eyed junco (*Junco hyemalis*), and pine siskin (*Carduelis pinus*) that is lacking in purely deciduous habitats.

Much of the plant and insect richness of mixed conifer/deciduous stands is also available in earlier shrub thicket stages, but the addition of taller trees makes these stands inviting to a wider range of wildlife. Moose and snowshoe hare peak in these successional stages, and consequently so do their predators, wolf and lynx (*Lynx canadensis*). Beaver can heavily influence the course of flood-plain succession by backwatering vast swamps full of snags for cavity nesters. They also selectively log cottonwoods from near-water communities, hastening the transition to open spruce woodland. In deciduous-fringed streams, more food is available to rearing fish than under purely coniferous cover (Wipfli 1997).

On the islands of Southeast, black cottonwood and willows are fairly unusual. This scarcity may be due in part to the higher numbers of deer that overbrowse them in the sapling stages. But these plume-seeded species also need bare mineral soil to germinate, and the smaller streams and rivers of the islands provide less raw alluvium than do those of the mainland. On Southeast islands, red alder is the common riparian deciduous tree.

Although the natural configuration of these streamside alder communities is linear, early

clearcutting in the mid-1900s created another type of red alder forest that covers much larger patches. Early clearcutting of spruce-dominated alluvial fans and flood plains often churned up the mineral soil so that red alder seeded in aggressively, temporarily out-competing conifer seedlings (Figs 46 & 51). Only the great tsunami wave of 1958 in Lituya Bay, has created red alder communities of such size (Lawrence 1979).

Summer wildlife habitat in a mature red alder stand is superior to that of equivalent-aged coniferous second growth. Mixed alder-conifer stands have more variable tree sizes, multiple canopy layers, understory plant diversity, wildlife cover, terrestrial invertebrates, and songbird nesting habitat (Duncan 2004). The high species richness and biomass of the alder stand understory contrasts greatly with the sparse understory of coniferous second growth (Hanley and Hoel 1996). In a Tenakee Inlet study of 28- to 39-year-old second-growth stands, the alder microsites had more enchanter's nightshade (*Circea alpina*), bedstraw (*Galium aparine*), foamflower, yellow violet (*Viola glabella*), and lady fern (*Athyrium felix-femina*) than were found in conifer microsites. As alder eventually dies out of a stand, the greater structural diversity continues to support better wildlife habitat. Associated small-mammal studies show superior conditions in red alder stands for Keen's mouse (*Peromyscus keeni*), common shrew (*Sorex cinereus*), and long-tailed vole (*Microtus longicaudis*) (Hanley and Barnard 1999). Estimated summer deer-carrying capacity is about 4.5

FIG 53 Even-aged spruce forest near the mouth of Bartlett River, Glacier Bay National Park. Oldest trees here, roughly 150 years old, have colonized surfaces that were deglaciated with the waning of the Little Ice Age. The post-glacial successional profile (Fig 49) shows the stages leading up to and following this "stem exclusion" phase.

FIG 54 Four stages of forest development in Southeast Alaska. Temporal overlap reflects site variability. (From Nowacki and Kramer 1998)


times higher in red alder stands than in equivalent-aged conifer stands (Hanley and Barnard 1998).

Initially, red alder delays the regrowth of Sitka spruce and lengthens the rotation age before a stand can be cut again. Red alder invasion of clearcuts has become less common since the 1980s for 2 reasons. First, today's yarding methods cause less soil disturbance, and soil is no longer exposed to alder germination over large patches. (Alder continues to colonize abandoned haul roads and channels of unbuffered streams in clearcuts [Fig 51].) Second, since the 1980s, clearcutting has shifted more to the upland hemlock forest, and remaining alluvial stands are now mostly protected by buffer restrictions.

Along the shores of Lynn Canal in northernmost Southeast, summer precipitation is low enough that stand-replacing wildfire can occur over intervals of a century or so (Fig 52). Mixed conifer/deciduous forests of spruce, lodgepole pine, cottonwood, and paper birch (*Betula papyrifera*) are found in this area. Although regionally rare, these birch "fire forests" in the transition zone to boreal interior climates are major contributors to the overall biodiversity of Southeast. The greatest richness of vascular plant species in Alaska centers around Skagway, a result of the overlap of coastal- and interior-adapted flora.

YOUNG, EVEN-AGED CONIFER

With the exception of the alluvial successional sequence (Fig 48), most maturing forests enter a
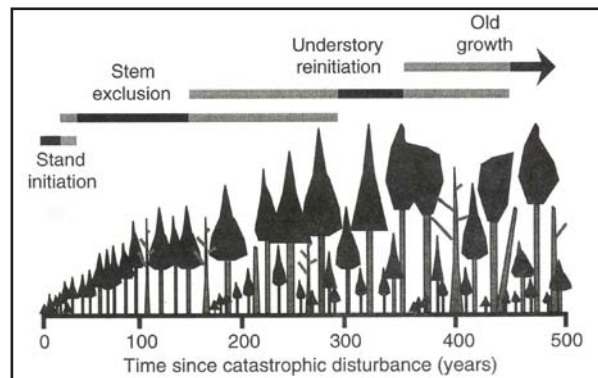
stage in which young, densely stocked conifers close canopy, shading out the understory (Fig 49, stage E; Fig 47, stages B, C, and D). From a forester's perspective, this shady second-growth has been called the "stem-exclusion stage" (Oliver 1981, Nowacki and Kramer 1998) (Fig 54) because the less vigorous overstory trees gradually die off and little colonization of tree seedlings can occur until the canopy begins to open up again. From a community ecologist's perspective, the young, closed canopy forest has been called the "depauperate understory stage" (Alaback 1984). Cover of shrubs and herbs drops to almost nil during this period, which may last for a century or more.

The timing of understory decline depends on "site index," or the speed at which the substrate grows trees. More productive sites experience earlier understory decline (Alaback 1982). Closed-canopy second-growth conifers have usually shaded out most of the understory by 25–35 years after disturbance.

FIG 55 Post-logging successional series. ***Upper left:*** Fresh clearcut west of Thorne Bay, Prince of Wales Island. A few ferns, shrubs and conifer seedlings have survived the logging activity. These will grow rapidly in the increased sunlight. ***Upper right:*** 1997 clearcut behind Fred Meyers in Juneau. Hemlock saplings are now head-high. Within the 3-meter-wide belt, shrubs cover 89% and forbs 34% of the ground. ***Lower left:*** This closed-canopy 36-year-old stand at Switzer Creek, Juneau, has 0.3% shrub cover and 0.02% forb cover within a similar belt. Even moss cover is only 13%. ***Lower right:*** forest of fast-growing spruce and hemlock on Heceta Island limestone that was clearcut by handsaw in 1926. Mosses and a few ferns grow, but almost no deer forage.

Most even-aged conifer forests in Southeast are the results of wind storms or logging, both of which are discussed below. Wind fells trees either by uprooting (windthrow) or stem breakage (windsnap). Collectively, the two forms of damage are referred to as blowdown (Harris 1989). Blowdown probably surpasses logging as the most widespread disturbance to forest communities across Southeast. It affects forests at all scales, from knocking down single trees to leveling entire stands.

Logging has likewise occurred at both coarse and fine scales. Before the advent of chainsaws in the 1940s, loggers tended to cut prime individual trees by handsaw along coastlines and rivers. This selective cutting, like single-tree or small-patch blowdown, altered the structure of old-growth stands but continued to provide better wildlife habitat than that of clearcut logging (Kirchhoff and Thomson 1998). The outcome of clearcut logging, which became the dominant cutting method in the 1950s, more closely resembles large-scale blowdown, resulting

in multi-acre patches of even-aged forest. Important differences between these natural and human-caused disturbances are discussed below, following descriptions of the 2 successional types.

The ratio of spruce to hemlock in even-aged coniferous forests depends on the nature of the disturbance. The most important factors in tree-species dominance are the degree to which soils are churned—exposing fresh nutrients to seed colonization—and the amount of shade cast by surviving trees, saplings, and shrubs. After glacial and alluvial disturbances, much bare mineral soil is available, giving fast-growing Sitka spruces an advantage over western hemlocks. In contrast, modern logging methods and many blowdown events can lead to hemlock dominance. This dominance happens because (1) insufficient bare soil is exposed to spruce seed colonization and (2) many young understory saplings are not blown down, or removed by loggers. The presence of these pre-existing hemlocks, called "advance regeneration," enables the hemlocks to

FIG 56 *Above:* Post-logging stand on outer Kosciusko Island, approximately 60 years old. Even-aged; closed canopy; vascular understory reinitiation has not begun and habitat value for most wildlife is low. *Below*: Old-growth stand on Kupreanof Island has large snags, trees of diverse size and age, multiple canopy layers with frequent gaps, and luxuriant understory of forbs, shrubs and hemlock saplings. Old growth has high habitat value for many species of fish and wildlife.

grow to dominate the subsequent forest. Because shade-intolerant spruces are rarely found as saplings in shady, mature forests, few of them are poised to inherit the future second growth.

Advance-regeneration hemlock is a major component of many post-logging and post-blowdown stands. In a study near Juneau, the majority of the hemlocks in the upper crown classes of a recovering blowdown forest originated from advance regeneration. Although none of these trees was much taller than 6 ft (2 m) at the time of disturbance, their initial advantage over new hemlock and spruce has been maintained for 120 years (Deal et al. 1991). In this way, disturbances like blowdown or logging can accelerate compositional changes toward shade-tolerant species (Spies and Franklin 1988).

At some point before a forest reaches true old-growth conditions, the canopy of even-aged forests begins to thin (Fig 47, stage D; Fig 63). More light reaches the understory. Shrubs such as blueberry and menziesia appear under gaps in the forest canopy, and herbs such as twisted stalk (*Streptopus* spp.), trailing raspberry, and bunchberry send vegetative runners through the mosses. This stage (Fig 54) is

called "understory reinitiation" (Alaback 1981, Oliver 1981). From this point on, the habitat conditions start improving for deer and other herbivores (Harris and Farr 1979, Wallmo and Schoen 1980, Alaback 1982, Rose 1984, Schoen et al. 1988).

Bird and mammal species affiliated with mature forests each respond to different stand features that may be regained on a different schedule than that of understory reinitiation. Marbled murrelets, for example, require large limbs for nesting. And cavity-nesting birds must wait until the maturing forest provides large snags. The evolution of these features may take several centuries.

Conifer seedlings and saplings also begin to appear in the maturing forest, but they may take longer than the herbs and shrubs to become widely reestablished. Nowacki and Kramer (1998) propose 2 substages within the understory-reinitiation stage. The first—herb and shrub recolonization—may be successful under small, ephemeral canopy gaps, whereas the second—conifer regeneration—is typically associated with larger gaps that cannot be quickly closed by lateral branch extensions.

Because of their widespread occurrence and

FIG 57 Logging on corporation lands at Big Salt Lake, Prince of Wales Island. The two fresh cuts framing the stream mouth are "second entries." Remnant conifers on the alluvial fan are themselves second growth from logging prior to ownership transfer. Behind the fan on gently rolling sedimentary and volcanic upland surfaces, moderately productive forests have also been recently logged.

The only ancient trees left in this scene are stunted hemlocks and cedars in forested wetlands.

FIG 58 Second-growth forest in Kanalku Bay, Admiralty Island. This stand burned 147 years prior to the photo. Trees are still strikingly same-sized, and understory reinitiation has scarcely begun. Although succession following fire is different from that following logging, sites like these do offer insights into the implications of forest management in Southeast. Photo by John Schoen.

ecological significance, blowdown and post-logging forests in Southeast have been topics of considerable research. From this work, it is possible to describe and compare these forest types.

Post-logging Forests

Because of long-standing concerns about effects of logging on wildlife habitat in Southeast, much research has been directed at post-logging vegetation development. Studies have addressed use of clearcuts by deer, bear, marten (*Martes americana, M. caurina*), wolf, goshawk (*Accipiter gentiles laingi, A.g. atricapillus*), forest songbirds, salmonids, and many other species (Schoen et al. 1988, Dellasala et al. 1996, Iverson et al. 1996, Murphy and Milner 1997, Titus et al. 1999, Person 2001). Habitat relationships of these

mammals, birds, and fish are discussed in Chapters 6, 7 and 8.

Post-logging succession resembles post-blowdown succession (described below) in many ways, but is somewhat less variable because logging targets a narrower range of forest types—the most highly productive stands—and usually results in complete removal of overstory canopy and all marketable logs. Factors influencing the successional pathway on clearcut lands include the following:

1. Pre-logging stand conditions such as ratio of spruce to hemlock, understory vegetation, and stocking of conifer seedlings and saplings.

2. Substrate: Most logging takes place on relatively well-drained surfaces, but succession differs on alluvium, karst, and upland slopes.

FIG 59 Until canopy closure, post-logging succession briefly provides increased browse. *Above*: In early May, a pair of pregnant does browse salmonberry in a fresh clearcut near Craig. *Below*: Cow moose in October uses fresh cut near Porcupine, north of Haines. (Some studies indicate that plants grown in open clearcuts may have lower nutritional quality than plants grown under a forest canopy [Hanley et al. 1987, Van Horne et al 1988].)

Successional patterns described below are based primarily upon studies of upland sites where hemlock was the original old-growth dominant. Post-logging succession on spruce-dominated alluvium is different. A few of these differences are noted below.
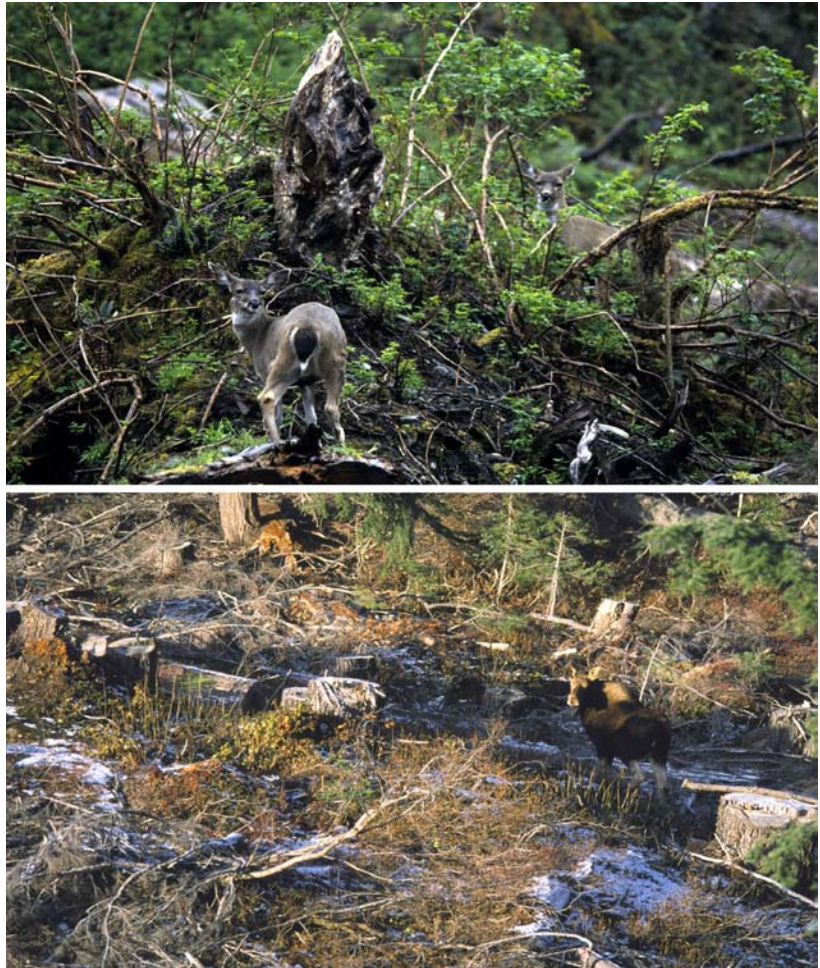
3. Elevation: The following generalizations apply to lowland forests. Post-logging succession at subalpine elevations in Southeast is much slower than at sea level.

4. Method of log removal: Tractor yarding exposes more soil than do A-frame, hi-lead, helicopter, or skyline systems.

For the first few years after logging, herbs are able to respond more quickly than shrubs. Low forbs like bunchberry and five-leaved bramble expand laterally, sending out shoots at rates of up to several yards (m) per year. Vertical growth of woody stems lags slightly behind forb expansion. But browsing pressure on blueberry has resulted in the ability of that shrub to quickly regrow stems from the large reserves of nutrients in roots. These reserves are also tapped by shrubs responding to increased light after logging. Therefore, the initial burst of herb cover wanes after about a decade as shrubs, and then conifer saplings, close cover over them (Alaback 1988).

The most depauperate stage in post-logging succession is shown in the 36-year photograph in Figure 56. At this time, the combination of complete shade with the steady litterfall of needles and branches can inhibit even mosses.

At 50–70 years, feather mosses expand across the forest floor. The dominant vascular plants are oak ferns (*Gymnocarpium dryopteris*), which die back in the winter. Moss cover peaks at 140–160 years. Compared to the successional patterns of other temperate rainforests, the second-growth conifer stands of Southeast are distinguished by the lack of understory development in intermediate stages. In contrast, an 80-year-old Douglas-fir stand in Oregon had already reached substantial understory development. In western Oregon, understory reinitiation begins after only 20–40 years. The young-to-mature western hemlock canopy of Southeast, however, is denser than almost any equivalent-aged conifer forest type to the south (Alaback 1982).

Clearcut logging has not been happening long enough in Southeast to precisely document understory reinitiation and the onset of improved wildlife habitat in this type of second-growth forest. Even in some of the oldest cutover stands, there is little hint of forb recolonization. Figure 56 shows a 77-year hand-logged clearcut, and Figure 58 illustrates a 147-year post-fire stand (in a presumably analogous

FIG 60 View northeast across Kasaan Bay to the Peninsula. Kassan Island (karst) in middle distance. On corporation land there is no required 1000-foot coastal buffer. Narrow buffer strips like these often blow down. There is hardly a patch of remaining old-growth in this entire scene larger than a few acres. Athough little can be done to influence logging policies on private land, a conservation assessment based upon watersheds and biogeographic provinces must account for these major impacts to fish and wildlife habitat. Tongass land management should take into account conditions on adjacent properties.

successional stage).

Predictions for post-logging stand development have been based largely on inference from more mature post-blowdown stands. The critical differences between these forest types are discussed below.

Few mammal or bird species respond positively to the stem-exclusion and depauperate-understory stages of post-logging succession in Southeast. The best studied species in regard to post-logging succession is Sitka black-tailed deer. Initially, deer are attracted in spring and summer to the flush of forb and shrub growth in open forest sites, forest edges, and fresh clearcuts. Clearcuts can be especially attractive to herbivores in uniformly forested country of low topographic relief where subalpine and coastal meadows are unavailable (Fig 59). But following canopy closure after 20–30 years, such stands have essentially no forage value to summering or wintering

deer or other herbivores for the rest of the timber rotation period. (In Southeast, 80–125 years is the anticipated time from logging to the next cutting cycle.)

In the next 100 years, if timber cutting proceeds as scheduled and as clearcuts shift into second growth, deer can be expected to decline substantially (Wallmo and Schoen 1980). Section 6.1 provides a more detailed discussion. On the southern islands of the archipelago, the decline of deer following canopy closure of second growth is expected to reduce numbers of the Alexander Archipelago wolf that preys primarily on black-tailed deer (Person 2001).

The influence of post-logging succession on other wildlife and fish species is examined in later chapters.

In an effort to better understand and eventually improve conditions for wildlife in second-growth forests across the Tongass, the USFS has invested

FIG 61 Blowdown forest at Eagle River, north of Juneau. Smooth-textured canopy in center is even-aged western hemlock forest dating to a major storm in 1883. In contrast, the coarse-textured canopy at top of photo is almost pure Sitka spruce growing on alluvium.

in experimental thinning projects (Hanley 2005). Silvicultural thinning is a proven method of improving yield and tree quality in second-growth stands. But pre-commercial thinning gives only a 10- to 20-year window of improved growth for understory herbs and shrubs (Alaback and Tappeiner 1991, Deal and Farr 1994, Russell 2005) and is very costly. Further, winter habitat values of thinned stands may be diminished if their canopies fail to intercept sufficient snow.

Post-logging succession on alluvial surfaces once dominated by big spruces appears to have been quite different from succession on upland hemlock sites. But differences are somewhat confused by the fact that yarding methods also typically differed. Concentrated logging on upland surfaces has mainly occurred during the past 2 decades, coinciding with the transition to less disruptive high-lead or skyline yarding. Rapid and complete canopy closure by conifers is the norm on

these sites.

In contrast, during the era of intensive alluvial-forest logging, from about 1950 to 1980, felled trees were usually dragged out by tractor, causing more soil disturbance and providing opportunity for red alder to colonize. This resulted in a mixed conifer/deciduous forest. As described above, these stands have a very different successional trajectory from pure conifer second-growth. (Hanley and Hoel 1996). But it remains unclear to what degree the differences are due to yarding methods as opposed to the fundamentally different substrates. Even in the absence of yarding disturbances, conifers show slower initial growth on alluvium than on upland sites (B. Schrader, Forest Ecologist, USFS, Juneau, personal communication, 2006) Also, the more prolific growth of salmonberry and alder on logged alluvium may "capture" a site,
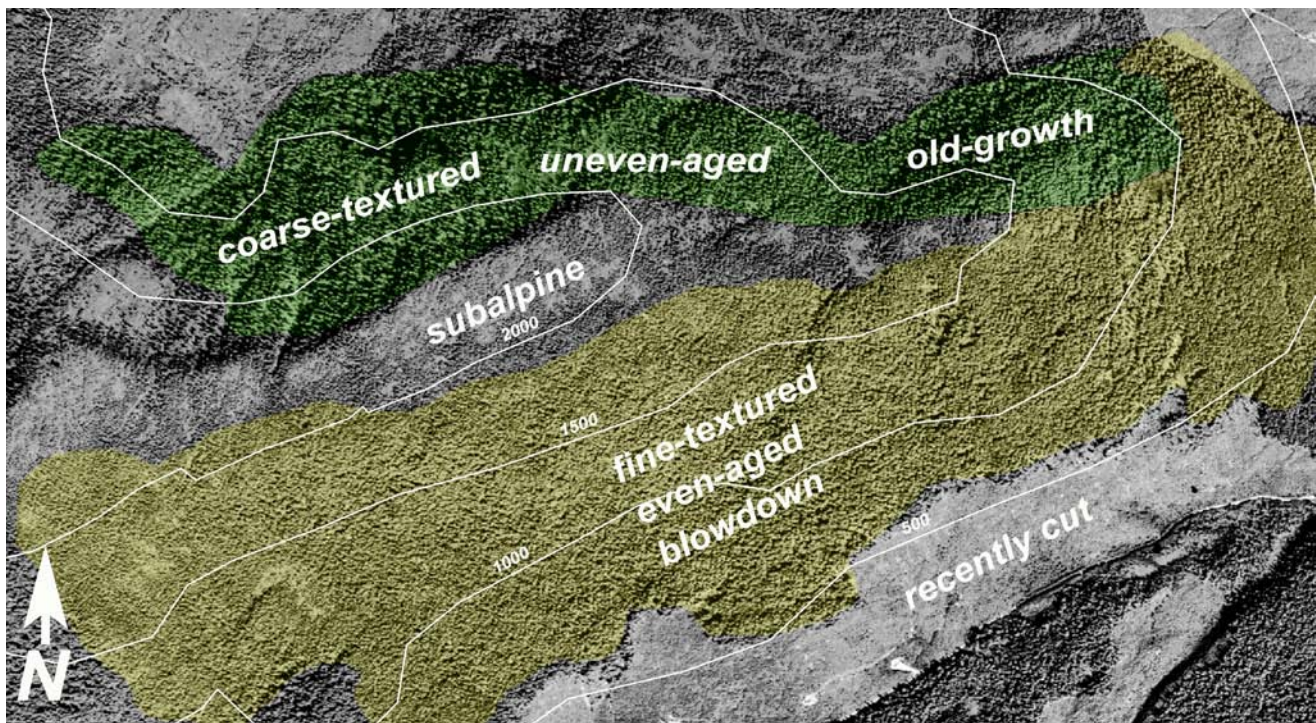
FIG 62 Topography and forest type on southern Mitkof Island. Digital orthoquad, 1996. Exposed, south-facing slopes are prone to blowdown, while north aspects are more protected. On this island most logging has been in the highly productive, wind-generated, even-aged forests.

shading conifer seedlings and resulting in delayed recruitment.

Moose have become rather widespread in Southeast in recent decades. Their expansion beyond the "traditional" willow/cottonwood habitat of hydrologically active mainland river corridors has been assisted by the proliferation of fresh clearcuts in otherwise conifer-dominated landscapes. An example is the moose colonization of the Thomas Bay alluvial plain to the north of Stikine River. Moose are able to browse these early successional cutover patches even in winter, when deer are excluded by deep snow. Like deer, however, moose will be unable to find forage in clearcuts after canopy closure is complete. The slower colonization of conifers on logged mainland alluvium may therefore work to the advantage of moose. In contrast, on islands such as Mitkof and Kupreanof where moose have also recently colonized, most young clearcuts are on upland sites. Here, moose will swiftly be edged out by closing conifer canopies. Because logging has declined in these areas, the ratio of stand initiation to stem-exclusion stages in cutover landscapes is swiftly shifting, to the detriment of moose habitat.

BLOWDOWN FORESTS

Studies in Southeast have addressed both the fine-scale gap dynamics of forests subject to low-intensity disturbance (Hocker 1990, Bormann et al. 1995, Ott 1997) and the coarse-scale patterns of high-intensity, stand-replacing blowdowns (Harris 1989, Kramer 1997, Ott 1997, Shepard et al. 1999, Kramer et al. 2000). The most comprehensive review of blowdown dynamics in Southeast is Nowacki and Kramer (1998).

In Southeast, blowdown forests tend to be concentrated on slopes exposed to prevailing southerly winds. Harris (1989) found that on Prince of Wales Island, the stands on windward slopes, flats, side slopes parallel to the direction of storm wind, and stands on broken topography were most susceptible. The aspects most likely to blow over were east to south, followed by west and southwest. North-facing aspects were only lightly damaged. Kramer (1997) found similar patterns on Kuiu Island.

Harris (1989) concluded that the forest types most vulnerable to blowdown are (1) uneven-aged with many rotten trunks, (2) tall with dense stocking on productive sites, (3) predominantly hemlock or spruce (not cedar or hardwoods), and (4) previously damaged

82 years

119 years

FIG 63 This wind-generated 150-year-old forest in Rocky Pass may appear uneven-aged at first glance, but tree coring has shown every tree to be about the same age; spruces are simply growing faster than hemlocks (M. Kramer, NASA, pers. comm. 1999). Structurally the stand has not reached old-growth status, but the combination of southerly aspect, good snow interception, and abundant blueberries and ground forbs makes this good winter deer habitat.

FIG 64 *Above*: Photo by Bob Smith, USFS, 1966. Forest recovering from nearly complete blowdown in 1883. The stand was still in the impoverished understory stage. *Below*: Repeat photo of the above in 2003. While an additional 36 years of succession caused relatively minor changes in stand structure, down logs have settled and rotted and understory reinitiation has begun. Blueberries now cover about 1/3 of the near and mid-distance.

by blowdown. Even-aged pole or young sawtimber stands are generally windfirm unless opened by partial thinning.

As a tree grows, its center of gravity becomes higher and more vulnerable. Mistletoe, insects, and fungi take their toll, weakening root systems and causing heart rot. The large majority of stands completely or partially blown down from 1961 to 1972 on Prince of Wales Island were considered to have reached old-growth conditions by the time of the disturbance (Harris 1989). The smooth, wind-shedding canopy of younger, even-aged stands gradually roughens as gaps appear. On the gap edges are trees that have grown up unprepared for this increased wind exposure.

As currently mapped, the Productive Old Growth (POG) includes a large but unknown acreage of wind-generated stands that do not qualify as old growth by most other definitions. Much of the POG does qualify as commercially and ecologically valuable forest, however. In places like Mitkof Island, most of the clearcut logging of the past 3 decades has focused on these relatively young (150–250 years), south-facing stands (Fig 62). (Doerr and DeGaynor, 2005)

Similarly, deer habitat can be excellent in some "middle-aged" wind-generated forests (Fig 63). In winter deer often select habitats with dense-canopy forests on south-facing slopes at elevations less than 1,000 ft (300 m) (Schoen and Kirchhoff 1990, Doerr et al. 2005). Some of this high-value forest is likely wind-generated pre-old growth. For deer, the turning point comes with understory reinitiation, not necessarily with the transition to old growth. Unfortunately, the onset of this stage is not detectable on aerial photographs. All fine-textured, even-aged forest stages look much alike from the air, whether the trees have only just closed canopy at 40 ft (12 m) (Fig 47, stage B) or tower more than 150 ft (45 m) tall (Fig 47, stage D). Until large gaps appear, it is difficult to judge stand height in stereophotography. Photointerpretation is quite adequate, however, for separating fine (young) and coarse-textured (older) stands.

Clearly, it is important to do a better job of mapping the "wind forest." In the meantime, Kramer (1997) has employed existing USFS data layers to develop a spatially explicit predictive windthrow model based on topographic exposure, soil stability, slope, and elevation. The model has been applied to Kuiu and Zarembo islands. Distribution of blowdown forests has also been mapped for northeast Chichagof Island (Ott 1997) and southeast Chichagof Island (Shepard et al. 1999). So far, however, blowdown mapping—either predictive or ground-truthed—is not available on a broader scale (Mapping Forest Structure sidebar).

Most studies of forest development after blowdown in Southeast have relied on inferences from chronosequences (comparisons of multiple stands of different ages) rather than following the progress of individual stands through time. Stand-reconstruction methods in old-growth forests (Deal et al. 1991) suggest that succession after blowdown may have as many alternative pathways as have been documented in post-glacial succession. Variable numbers of overstory and subcanopy trees are left standing after damaging windstorms, increasing structural heterogeneity in subsequent forest development. And much depends on initial understory composition.

Blowdown has been common in the past and may increase in the future. With global warming,

strengthening thermal gradients across the land/sea interface may lead to greater intensity and duration of windstorms (Alaback and McClellan 1993).

DIFFERENCES BETWEEN BLOWDOWN AND CUTOVER FORESTS

Clearcutting differs from natural disturbances in several basic ways (Spies and Franklin 1988):

• **It removes coarse woody debris** (CWD) and the big live trees that continue to produce CWD over time. Under short rotations, CWD declines further, reducing site productivity and important fish and wildlife habitat components.

• **It increases fragmentation** of natural forests, resulting in smaller patch sizes of remnant forest than does fire or blowdown disturbance.

• **The standard timber rotation** (80–125 years in Southeast) will truncate forest succession well before old growth begins to develop.

Clearcut logging removes almost all conifers and disturbs or crushes many saplings and seedlings. In contrast, many surviving trees may be left after blowdown, giving the successional process a head start.

Equipment used in logging leaves behind a different understory than that of blowdown disturbances. Machine entry in a stand reduces diversity because heavy equipment fragments and scatters rotten wood in the advanced stages of decay. Trees not removed are bunched and aligned along the direction of skidding. Fewer kinds of organisms can thrive in the resulting microhabitats (Maser and Trappe 1984).

Nowacki and Kramer (1998) compared logging to blowdown disturbances in Southeast. They cautioned that clearcutting can be a problem on wind-protected landscapes where small-scale gap processes originally prevailed (blowing down of individual or small groups of trees). Cuts of typically more than 40 acres (16 ha) under 100-year rotation keep the forest in the first 2 stages of development—stand initiation and stem exclusion—but never attain understory reinitiation. Few blowdowns result in complete overstory removal, and much of the forest legacy (dead wood, standing and down) remains. "Large, simply configured clearcuts reduce landscape diversity, sever forested wildlife corridors, and curtail

gene flow as well as fragmenting, isolating, and reducing old-growth patches. These effects may be most pronounced in areas already consisting of highly fragmented forest mosaics," according to Nowacki and Kramer (1998). Many understory species invest considerable energy in their root systems, colonizing mostly vegetatively. They drop out of stands under short rotations (Nowacki and Kramer 1998).

Other differences between logging and natural disturbances that have been seen as positive in terms of timber yield may have long-term negative consequences for forest structural diversity and ecosystem processes. In the short run, clearcuts reduce heart rot and hemlock dwarf mistletoe. But heart rot and mistletoe play key roles in small-scale gap processes in old-growth forests and provide unique habitat features. On wind-prone landscapes, clearcutting differs from blowdown in the removal of woody biomass and the lack of deep soil churning. The latter may lead to paludification (waterlogging) through formation of impermeable soil layers. By comparison with uprooting from windthrow, even tractor yarding results only in light surface disturbance (Nowacki and Kramer 1998). Although clearcutting has been described by some forest managers as emulating natural disturbances, ecologically it is very different.

On northern Kuiu Island, more than 50% of clearcuts are in areas where small-scale gap processes (largely small blowdown events) predominate, and only 20% (5,000 acres [2,023 ha]) are in areas where large-scale blowdowns predominate. After blowdown, surviving trees serve as seed sources, habitat structures, and shade for light-sensitive plants. On northeast Chichagof Island, the blowdown rate has been relatively constant since the 1700s, with just one big spike in the 1890s that affected 3% of the Productive Old Growth (POG). Clearcutting since the 1960s has been a departure from this pattern, with 9% of the POG removed in the 1990s alone. Studies on various parts of Chichagof show that: "The clearcut area has exceeded the area that blew over by some 4 to 17 times on Chichagof Island" (Nowacki and Kramer 1998).

To mimic natural disturbances, Nowacki and Kramer (1998) recommend 5 management options:

1. Use single-tree or small-group selections in areas where gap-phase processes predominate

2. Leave remnant trees in densities consistent with natural blowdown

3. Decrease clearcut unit size and frequency and locate units in wind-exposed landscapes

4. Extend rotations into understory reinitiation stages (i.e. wait longer before cutting again)

5. Consider topography in layout of both cutting units and old-growth reserves. Wind protected sites are the best prospects for the latter.

Kirchhoff and Thomson (1998) also recommend selective harvest as an alternative to clearcutting because it better maintained more of an old-growth structure and productive understory plant community. Of course, all these options would reduce the amount of timber volume cut in any given year.

Mountain Zones

With increasing elevation, winter snows deepen and growing seasons contract. Plant communities change in response to these climatic controls. Above the coastal forest dominated by western hemlock, a sequence of elevational zones includes: small-tree subalpine forest; subalpine parkland; and alpine tundra (Figs 65, 66). Wildlife values change accordingly.

"Forest limit" refers to the upper limit of closed subalpine forest. Conifers above this line occur as scattered clumps of stunted "elfinwood." The highest of these dwarf conifers at "tree limit" can reach 3,500–4,000 ft (1,050–1,200 m) on some mountains.

High elevation habitats of Southeast have received very little scientific study. This report follows the elevational zones described by Brooke et al. (1970) for southwestern British Columbia.

SUBALPINE FOREST SUBZONE

The subalpine zone or belt is defined as "the forest-tundra ecotone, with dwarfed tree growth and subalpine meadows (Löve 1970). Brooke et al. (1970) have subdivided this zone into the subalpine forest and subalpine parkland subzones. The lower limit of the subalpine is a subtle and easily missed transition that occurs about halfway from sea level to tree limit throughout most of Southeast. Here, western hemlock-dominated forests grade into stands of smaller mountain hemlock (*Tsuga mertensiana*), the conifer best adapted to cool summers and deep, wet, winter snow conditions. The transition to this subalpine forest zone usually occurs at about 1,500 ft (450 m) above sea level, but can be as low as 1,000 ft (300 m) in places like Glacier Bay, where all elevational zones were depressed during the colder, snowier winters of the Little Ice Age.
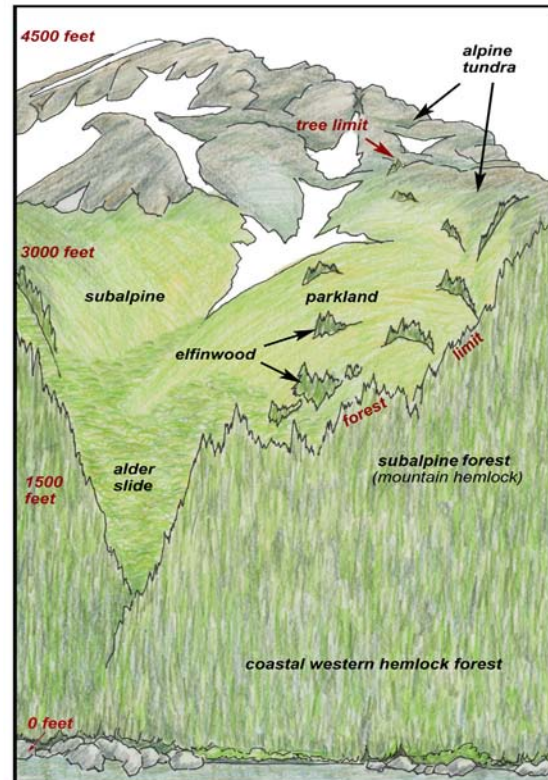
FIG 65 Sequence of elevational belts on a typical Southeast mountainside. Communities also respond to aspect and topography; transitions are lower on north slopes or in valleys and higher on south slopes and buttresses.

FIG 66 Elevational belts on the shoulder of Mount Hawthorne near Juneau. In this location the alder thicket zone is very wide, perhaps due to the Taku winds that bring severe interior weather conditions in winter, depressing the forest limit.

FIG 67 Common flowers of the lush subalpine meadows. From top to bottom: broad-petalled gentian (*Gentiana platypetala*) and fir clubmoss (*Lycopodium selago*); whorled lousewort (*Pedicularis verticillata*) and monkshood (*Aconitum delfinifolium*); narcissus-flowered anemone (*Anemone narcissiflora*). Rapid summer growth in the subalpine meadows makes this belt extremely important to grazing deer, bear and mountain goats.

FIG 68 Mother blue grouse takes to a low spruce branch, attempting to distract the photographer from half-grown chicks. Grouse broods are common at montane elevations.

On the climb upward, trees become shorter and often more widely spaced. In response, shrubs like blueberry and salmonberry become more abundant. Because winter snow depths usually exclude deer from the subalpine forest subzone, browsing pressure on blueberries is reduced, a further encouragement to proliferation of the shrub layer. Depending on topography and soil drainage, this subalpine coniferous forest gradually breaks up into small, ferny openings that are excellent summer habitat for herbivores and insectivores. False hellebore (*Veratrum viride*) appears in these subalpine glades.

Blue grouse (*Dendragapus obscurus*) broods seem to be especially common at these upper forest limits (Fig 68), probably because lush shrub and herbaceous thickets offer a high abundance of insects and good hiding cover for the growing chicks. High densities of grouse in turn attract northern goshawks to the subalpine elevations; young blue grouse are a favored prey species for these forest-hunting raptors. Likewise, early summer song intensity of breeding birds like dark-eyed juncos (*Junco hyemalis*), ruby-crowned kinglets (*Regulus calendula*), and Wilson's warblers (*Wilsonia pusilla*) can be very high. In spite of the late green-up relative to sea level, these birds manage to quickly fledge broods in the productive timberline forests.

In winter, tracks of marten and short-tailed weasel (*Mustela ermina*) are abundant in the high subalpine forests. Their key prey species—Keen's mouse, red-backed voles (*Clethrionomys rutilis and C. gapperi*), and long-tailed voles—respond favorably to the rich subalpine herb and shrub layers. For these small rodents, the deep snows that exclude deer in winter may actually be a positive factor, providing thermal cover and partial protection from predators.

Although deer are forced down from the high country in fall and early winter, the subalpine forest and parkland subzones are seasonally very important to them. In portions of Southeast, some deer seem to spend their annual cycle following the snow line up and down the mountainsides. After heavy fall rains that briefly remove snow, deer climb again, staying as high as snow conditions allow, indicating greater food availability at these higher elevations (Schoen and Kirchhoff 1990). There may also be less predation from wolves in the high country (Person 2001)

Some mountain goats take cover from severe winter storms by retreating from ridge-top habitat into cliffy sections of subalpine forest where snow is partially intercepted by the hemlock canopy (Schoen and Kirchhoff 1982, Fox et al. 1989).

FIG 69 Yearling buck in subalpine meadow. In complex mountain topography some meadows are available to grazers in May, while other places retain snow into August. This means that deer can always find tender, freshly uncovered greens, following spring-like conditions throughout the summer.

FIG 70 Inset: small-flowered paintbrush (*Castilleja parviflora*) and deer cabbage (*Fauria crista-galli*).

FIG 71 Hoary marmot (*Marmota calligata*) in damp subalpine sedge meadow. Marmots cannot range as widely as deer, and therefore have more intensive and localized effects on their favored forage plants.

Telemetry studies of brown bears indicate that most denning takes place within the subalpine forest subzone. Mean den elevation for 120 collared bears was 2,100 ft (640 m) and slope averaged 35 degrees. Dens were found in caves or excavated in the root structure of big old-growth trees (Schoen et al. 1987).

Genuine old-growth trees can occur at any elevation from sea level to tree limit. Ancient stands of spruce and mountain hemlock may stand only 30 ft (10 m) tall, with trunks no thicker than a person's waist. Yet their tightly packed rings indicate that some of these trees were already old at the peak of the Little Ice Age about 250 years ago. Even the stunted elfinwood patches at tree limit, scarcely tall enough to hide a deer, may contain old-growth trees.

SUBALPINE PARKLAND SUBZONE

Above the closed subalpine forests, several possible transitions to higher communities occur (Fig 65). The sequence depends on topography, drainage, and snow dynamics. Studies in southern coastal British Columbia (Brooks et al. 1970), where mountain climate is similar to that of Southeast, show that on an elevational transect, winter snow depth peaks in the subalpine zone and declines thereafter into the alpine. The coastal snow pack is much denser and wetter than in the cold interior mountains, and it creeps slowly downslope in late winter and spring ("snowcreep"), eliminating woody-stemmed vegetation from many microhabitats. Saturated soils also slip downhill at much slower rates, inhibiting growth of trees and even shrubs.

The result is a mosaic of lush subalpine meadows and increasingly dispersed stands of dwarfed conifers, a distinctively maritime herbaceous mountain community. Because the meadow plants die back to their root systems in the fall, they are immune to the snowcreep that removes blueberries, alders, and conifers. The deep snow pack protects subalpine herbs from the harsh winter wind and cold that make higher alpine habitats (described below) a place of stress and desiccation.

Although the growing season is short in the subalpine subzone, daylight hours at Southeast latitudes are almost unending at the time of summer

August 1949

Donald Lawrence

August 2004

FIG 72 Sitka alder invasion of subalpine meadow over 55-year interval at 1,900 ft (274 m) on Mount Roberts, above Juneau.

Southeast mountains, these herbivores include deer, bear, mountain goat, and hoary marmot (*Marmota calligata*) (Fig 71), and mature grouse and ptarmigan (*Lagopus spp.*) The young birds are insectivorous but also find abundant prey in these communities. Although Sitka black-tailed deer are very eclectic feeders, deer cabbage (*Fauria crista-galli*) is probably the most important summer food for migratory deer (Fig 70). Deer cabbage is the dominant plant of many subalpine bowls in places such as Admiralty Island.

Radio telemetry studies of deer on Admiralty Island show that as snow pack recedes in late spring, deer move out of old-growth forests into scrub stands and moist subalpine meadows, gradually making greater use of north faces (Schoen and Kirchhoff 1990). Highly dissected relief creates microsite diversity that allows selection of various growth stages. In September, deer cabbage and other summer herbs wilt and lie down, turning the mountain meadows a lovely (but slippery) gold. At that point, herbivores focus their feeding in subalpine forests.

Although most brown bears concentrate on lowland salmon streams in late summer, a smaller fraction of the population, mostly sows with cubs, stay in the high country throughout the snow-free season (Schoen et al. 1986, Ben-David et al. 2004). These bears, and others making shorter visits to the mountains, forage primarily in the subalpine zone.

For deer and bear, the lower portions of the subalpine zone offer not only exceptional forage but often an ideal interspersion of open grazing areas with small stands of spruce and hemlock for hiding and thermal cover. With increasing elevation, the conifers

solstice. The plants best able to take advantage of the combination of prolonged summer sunlight but brief growing season are those that can grow to full height in a few short weeks. These plants include many species described previously in the coastal uplift meadows such as fireweed, lupine, (*Lupinus nootkatensis*) cow parsnip, bluejoint (*Calamagrostis canadensis*), and flowers in the sunflower family (Asteraceae). Species more distinctively subalpine in distribution are narcissus-flowered anemone (*Anemone narcissiflora*), various louseworts (*Pedicularis spp*), and broad-petalled gentian (*Gentiana platypetala*) (Fig 67).

Subalpine meadows also resemble coastal uplift meadows in their attraction to grazers. Rapidly growing herb communities are the most desirable of all foraging places for most herbivores. In

FIG 73 Late snowbed surrounded by alpine heather community in the mountains above Juneau. Gastineau Peak in background is 3666 ft (1118 m) elevation. Microtopography strongly influences where snow collects and how long it persists. Combined with the very short growing season this results in a distinctive mosaic of plant associations with sharp boundaries.

FIG 74 Cooley buttercup (*Ranunculus cooleyae*), an alpine species first discovered near Juneau, restricted to the moist coast range mountains.

grow more stunted; extensive elfinwood copses occur on convex topography free of winter snowcreep. These shelter not only mammals but also nesting songbirds like American robin (*Turdus migratorius*) and fox sparrow (*Passerella iliaca*).

Because mountain goats cannot outrun their predators, they are restricted to the proximity of cliffy escape habitat. But they take advantage of subalpine meadows wherever these occur close to bedrock faces.

Sitka alder thickets are common on steeper subalpine slopes. On some especially active mountainsides, these avalanche-induced thickets may extend from summit to sea level.

The subalpine is the most sensitive of the elevational zones to climatic change. Since the ending of the Little Ice Age, warmer, longer summers and earlier snow melt have promoted shrub invasion of subalpine meadows (Fig 72). This changing vegetation will affect the foraging habitat for many herbivores, and will alter nesting habitat for songbirds.

ALPINE TUNDRA ZONE

Arctic and alpine ecologists throughout the world have noted that trees are generally unable to grow where the mean temperature for the warmest summer month is cooler than 50°F (10°C). Above (or northward from) this 50°F (10°C) isotherm lies a slow-growing, very conservative community called "tundra." In many places, the highest (or most northerly) trees grade directly into tundra.

In Southeast, however, these elevational zones are more typically separated by lush subalpine meadow communities. The reason appears to be that Southeast conifers rarely reach the 50°F (10°C) summer isotherm line. Tree limits and forest limits are depressed here from such causes as snowcreep, frequent avalanches, and the recent influences of the Little Ice Age. In place of the highest subalpine forest, the rich herbaceous meadows grow.

The true alpine zone is higher (Figs 65 & 66), at

FIG 75 Common alpine plants - clockwise from upper left: alpine azalea (*Loiseleuria procumbens*) and roseroot (*Sedum integrifolium*); purple mountain saxifrage (*Saxifraga oppositifolia*); Alaskan moss heather (*Cassiope stelleriana*) and reindeer lichen (*Cladonia sp*); moss campion (*Silene acaulis*).

FIG 76 The list of truly alpine-adapted fauna in Southeast is short. The most successful are–from top to bottom– mountain goat (*Oreamnos americana*), rock ptarmigan (*Lagopus mutus*), and American pipit (*Anthus rubescens*).

elevations where winter snows are colder, drier, and more easily redistributed into massive drifts and cornices. As this snow melts in spring and summer, it uncovers the convexities first and the concavities last (Fig 73). An intricate patchwork of distinctive microcommunities results from the staggered timing of plant maturity and associated variations in drainage.

On windy sites, many little knobs and ridges are blown clear of snow even in mid-winter. These are the harshest terrestrial microsites in Southeast. Plants here must be able to endure severe desiccation. They are ground-huggers only a few inches (cm) tall, generally with small, leathery leaves (Fig 75). In summer, the flowers of these microsites seem huge by comparison to their foliage. During winter, mountain goats often forage on these windblown ridges, remaining close to escape terrain (Schoen and Kirchhoff 1982).

Mountain heathers (*Phyllodoce glanduliflora* and *Cassiope* spp.), along with other tough-leaved plants like arctic willow (*Salix arctica*), crowberry (*Empetrum nigrum*), and partridgefoot (*Luetkea pectinata*), dominate most of the Southeast alpine tundra. Few of the true alpine plants are very palatable to the large herbivores of Southeast, which tend to prefer the more succulent subalpine "gardens." The

heather tundra is laced with game trails, however. Mountain ridges are favored thoroughfares not only for deer, goat, and bear, but also for wide-ranging Southeast predators, the wolf and wolverine (*Gulo gulo*). The latter is largely restricted to alpine and subalpine habitats in Southeast, where it hunts mostly for marmots and ptarmigan.

Alpine tundra feels like paradise on a warm, still summer day. But even in summer, wind, rain, and overcast skies are the norm in the Southeast high country. Few birds nest here. The 2 most successful species are rock ptarmigan (*Lagopus mutus*) and American pipit (*Anthus rubescens*) (Fig 76).

REGIONAL VARIATION IN SOUTHEAST MOUNTAIN HABITATS

The above descriptions of elevational zones portray a "generic" Southeast mountain environment, based mostly on experience in the Juneau area. Plant distributions and community ecology of Southeast mountain habitats are poorly documented, however. Regional variation can be striking, and depends on such factors as bedrock type, maritime versus interior climate, deer herbivory, and response to warming conditions since the recent Little Ice Age, which was
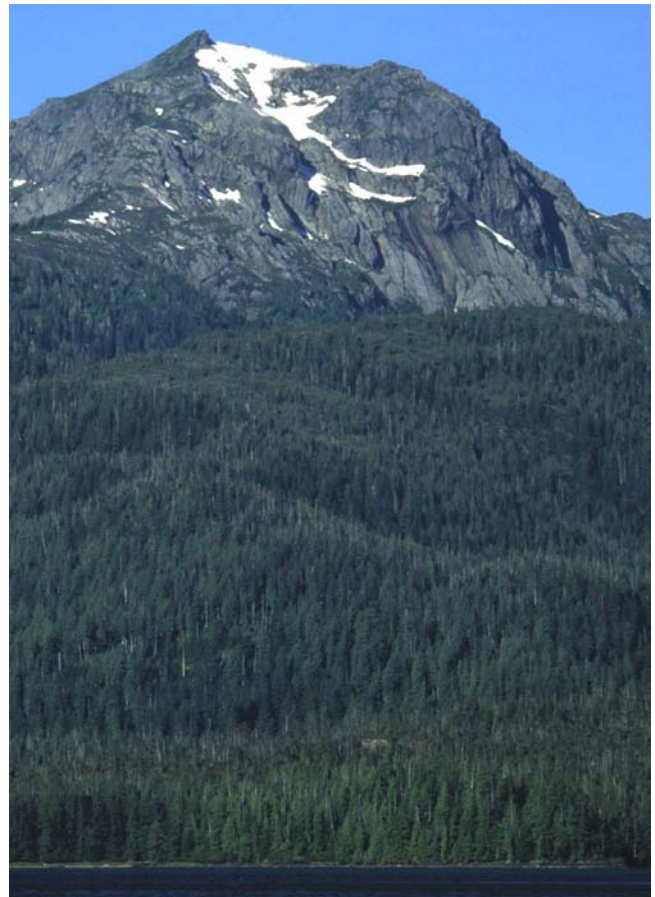
As in lowland forests, mountain habitats show extremes in productivity and species composition depending on bedrock type. **FIG 77** Left: view southward toward the Couverden Islands in the southern Chilkat Range. "Dimpled" topography at 2,000 feet (600 m) in foreground is from dissolution of Silurian limestone bedrock causing sinkholes that are overgrown with rich alder/salmonberry thickets.

FIG 78 Right: Mount Etolin, 3,270 feet (1000 m), highest summit in South Etolin Island Wilderness. Like most Wilderness designations in Southeast (Admiralty excepted) this one is predominantly on granite, and has low-productive forests of little interest to the timber industry. High-country communities are relatively spartan, and ridgetops are almost entirely lacking in lush subalpine meadows.

most pronounced in northern Southeast and near the large mainland icefields.

Southeast-wide surveys of mountain habitats should be a conservation priority. The available information permits a few initial observations about regional variation.

Bedrock Type is very important in mountain habitats. Granitic rock (Fig 78) does not weather into soils suitable for rich subalpine meadows. Alpine plant diversity is relatively low, and forage for herbivores is minimal. For example, on Mud Bay Mountain, 3,015 ft (919 m), capping a Cretaceous batholith on northern Chichagof Island, summer deer use of the high country is very low compared to deer activity on nearby metamorphic and sedimentary ranges.

Mountain communities on highland karst are harder to characterize. In some places, especially where terrain is rolling and not too steep, extensive herbaceous meadows are found on solution-pitted karst. Deer summering in these karst meadows are some of the largest in Southeast (J. Baichtal, Geologist, USFS, Ketchikan, AK, personal communication 2001). In other mountain communities (Fig 80), the subalpine transition may be completely lacking, and the cover of alpine plants is very sparse. Some karst species, however, are regionally rare calcicoles, like androsace (*Androsace lehmanniana*) (Fig 79).

Snow melts earlier and summer conditions are drier on limestone alpine habitats (Jacques 1973). On these porous, excessively drained surfaces, a dry spell of only a few weeks duration may kill all but the most drought-tolerant species. Comparing carbonate to noncarbonate rock habitats on the mountains of Prince of Wales Island,

FIG 79 Three species of limited distribution in the mountains of Southeast: *Top* subalpine fir at 3000 ft (900 m) in White Pass above Skagway. A true fir, this interior species is found along the Canadian border, and on some southern islands; *Middle* sweet-flowered androsace (*Androsace lehmanniana*), a widespread boreal "calcicole" known in Southeast only from isolated karst mountaintops in the Chilkats and Prince of Wales area; *Bottom* broad-leaved marsh marigold (*Caltha biflora*) restricted in our region to the southern islands, where it is an important deer forage species along with the similar-looking deer cabbage.

FIG 80 Karst summit at 2200-ft (640 m) on Lemesurier Island at the mouth of Glacier Bay. Soils are thin and dominated by heather species unpalatable to wildlife. Subalpine meadows are almost non-existent. Crevices under the heath mats in foreground descend into the dissolving limestone.
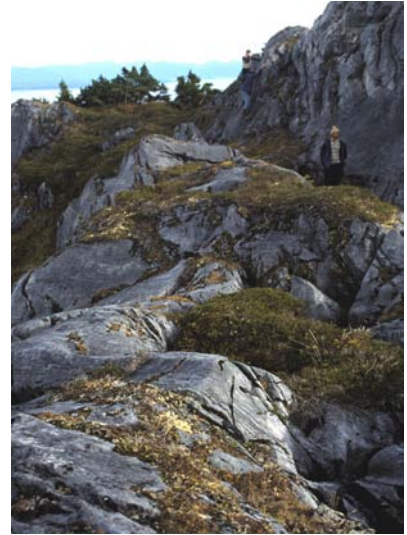
Jacques (1973) found strong differences in species composition.

Another regionally uncommon bedrock type with distinctive flora is ultramafic rock, such as that found on Mount Burnett on the Cleveland Peninsula. Kruckeberg's holly fern (*Polystichum kruckebergii*) is a rare endemic species known only on this rock type (USFS 1997).

Climate influences on mountain plant communities have received little attention in Southeast. Because these communities occupy a much more stressful climatic regime in both summer and winter than that of the lowland forests and wetlands, floristic gradients from north to south and from outer coast to mainland are stronger in the high country than at lower elevations. These climatic influences may be difficult to separate from others such as herbivory and post-glacial colonization patterns.

Herbivory is intensely focused on certain subalpine deer pastures in places like Admiralty Island. Large basins there often support near monocultures of deer cabbage (Fig 69, inset), densely laced with deer trails. These meadows are mowed, trampled, and fertilized. On a more localized scale, marmot grazing and digging can have pronounced effects on vegetation.

Post-glacial Colonization rates and source areas have varied between species. As in the lowlands, certain mountain species are confined to southern Southeast. The broad-leaved marsh marigold, (*Caltha biflora*) for example (Fig 79), is abundant in damp subalpine meadows on Prince of Wales. It probably could grow as well in similar high-country meadows of northern Southeast, but has simply not had time to colonize in the several millennia since deglaciation and warming climate created suitable subalpine habitat.

In southern Southeast, isolated mountainous areas were never overridden by ice during the last great ice age. These refugia may have supported subalpine fir and as many as 42 species of plants with discontinuous populations that have slowly expanded their ranges following deglaciation (Jacques 1973).

One result of these regional variations in habitat and history is the strong probability that as-yet undiscovered species and subspecies of flora and fauna exist in the mountains of Southeast. Only by thorough and wide-ranging surveys will the complexity of the Southeast mountainous archipelago be fully recognized.

Poorly Drained Habitats

The 4.5 million acres of freshwater wetlands mapped by the National Wetlands Inventory (NWI) on the Tongass comprise about 26% of its land area. This abundance of wetlands may not be apparent from a boat; when scanning the shores from a sea-level perspective, observers face a wall of apparently endless forest. But from the air, an extensive patchwork of wet openings can usually be seen, especially on flat or gently rolling terrain. The colloquial term for such wetland is "muskeg," a colorful but rather imprecise term borrowed from boreal regions, where muskeg originally defined soggy black-spruce communities on permafrost (T. Brock, retired Wetlands Ecologist, USFS, Juneau, AK, personal communication 1998). The following descriptions apply more technically correct terms in general use by wetland ecologists across North America. As it turns out, the habitats lumped as muskeg in Southeast include very distinctive communities, with widely differing values for wildlife.

Some of these wetlands—freshwater marshes and wet meadows—are relatively young. Others—fens (dominated by deep sedge peat) and bogs (mostly with sphagnum moss peat)—are so ancient that old-growth forests seem like newcomers by comparison.

It is often hard to precisely distinguish between forest and wetland. On surfaces of intermediate drainage, the NWI shows "forested wetlands," scrubby, unproductive
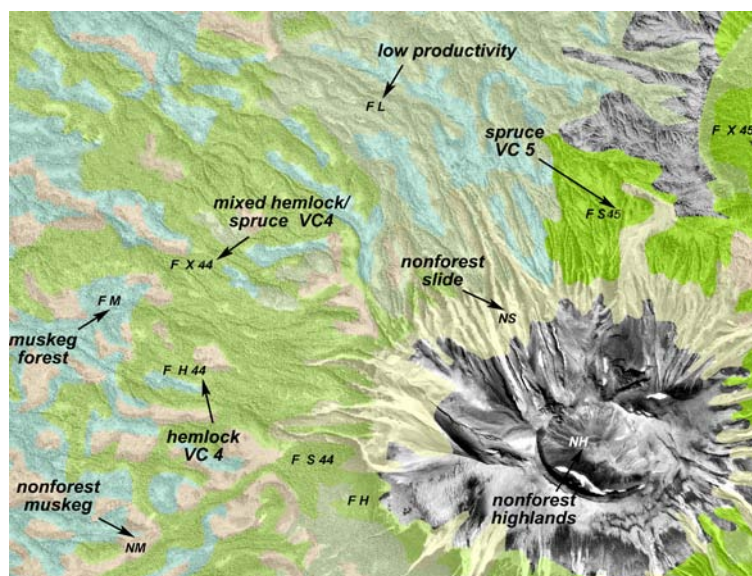
FIG 81 Mosaic of small-tree forest and peatland northwest of Mount Edgecumbe, Kruzof Island. On this TIMTYP map the small tree forest is shown by the combination of volume class 4 (eg. F H 44, intermediate green color) and low-productive forest (FL, palest green).

stands on poorly drained soils. These habitats share more structural features with old-growth forest than with open peatland but are described here because they are genuine wetlands.

WET, SMALL-TREE FOREST

On flat or gently sloping, poorly drained surfaces such as raised marine terraces and subalpine benches, scrub forests of short, widely spaced trees are common. On the original TIMTYP map, these forests are shown as volume class (VC) 4, ranging from 8,000 to 20,000 mbf/a. VC 4 constitutes fully 50% of the Productive Old Growth (POG), or "commercial forest."On the more recent tree-size map (Fig 81), the wet, small-tree class is delineated by the intersection of the TIMTYP VC 4 with forested wetlands as shown on NWI

FIG 82 Open woodland of dwarfed shore pines on unproductive granitic bedrock. Baker Island west of Craig.

maps. The NWI was used because only this database completely maps soil wetness for the entire region, including wilderness areas such as Admiralty Island and Misty Fiords. Because NWI-mapped forested wetlands are often fairly small, scattered patches, the small-tree forest on the tree-size map is much less extensive than VC 4 on TIMTYP.

Tree species diversity is higher in the wet scrub forest than in more productive stands where spruce and western hemlock dominate. In the small-tree forest, cover is shared more equitably among western and mountain hemlock (*Tsuga heterophylla* and *mertensiana*), yellow-cedar (*Chamaecyparis nootkatensis*), western redcedar (*Thuja plicata,* restricted to the southern Tongass), shore pine (*Pinus contorta*), and Sitka spruce. The short, well-spaced trees allow plentiful light to penetrate to the shrub layer, which is often dense enough to discourage human hikers. Species richness and structural complexity in moss, herb, and shrub layers is also greater in small-tree forests than in more productive (hence, shadier) stands.

Small-tree forests often form transitional "halos" around more open peatland, or conversely, around islands of bigger trees in a peatland matrix. Much brushier than either the peatlands or the tall-tree forests, these ecotones also have greater blueberry production, and become important midsummer foraging zones for bears. Similarly, in studies by the ADF&G, scrub forests were used substantially by radio-collared deer in late spring, summer, and early fall (Schoen and Kirchhoff 1990).

Summer bird-banding programs and breeding bird surveys on Chichagof Island indicate that some types of songbirds such as brush-nesting warblers and sparrows may be more abundant in dispersed, shrubby stands of small trees than in shadier, taller forests with more poorly developed understories (C. Pohl, Biologist, Juneau, AK, personal communication 2005).

On gently rolling lowlands like central Cleveland Peninsula, Pleasant Island, western Kupreanof and southern Kruzof islands (Fig 81), small-tree forests stretch for miles in an interlacing mosaic with peatland. Only the V-notch gullies of streams contain narrow stringers of taller trees on steeper, better-drained slopes. The scrub forests are ancient and have

FIG 83 The wet, small-tree forest often forms "halos" acround more open bogs or fens. Here at Threemile Arm on Kuiu Island, the forest transition is "feathered," with waist-high foreground pines grading to wet-footed scrub hemlock and cedar in distance. Dead tops are from yellow-cedar dieback, described in the preceding section on cedar forest.

FIG 84 Aerial view of scrub forest and peatland near Swan Cove, Admiralty Island.

changed little for thousands of years. Open-grown, small trees with scruffy canopies are generally quite windfirm, and stand-replacing blowdown is nearly impossible. Because old or dead trees on these sites tend to snap rather than uproot, increasingly sterile peaty soils are rarely churned and hardpans develop, further elevating the water table.

Succession is hard to study in small-tree forests because change is extremely slow and major disturbances are rare. In contrast, disturbances to the large-tree forest are ongoing and observable; with logging, glaciation, or blowdown, examples of beginnings, mid-points, and culminations of community development can be identified. With small-tree forest succession on wet, nutrient-poor substrates, one can only speculate based upon evidence from ancient soil profiles. Two disturbances that initiated succession toward the small-tree forest were post-Wisconsin deglaciation, and uplifting of ancient marine terraces about 9,000 to 14,000 years ago.

Radiocarbon dates from peat cores in bogs below Mount Edgecumbe on Kruzof Island indicate 3 major Holocene landscape types: 1) deciduous woodland from 9,000 to 6,000 years BP; 2) small-tree coniferous woodland from 6,000 to 3,000 BP; 3) a shift toward peatland from about 3,000 to present (Klinger et al. 1990). The latter 2 land-cover types still share the lowland volcanic plain surrounding Mount Edgecumbe (Fig 81).

Lake-bed cores on Pleasant Island near Glacier Bay show that Sitka spruce was replaced by western and mountain hemlock—probably a small-tree forest—between 9,000 and 7,000 BP, coinciding with progressive accumulation of organic material

in the soils. In the absence of large-scale blowdown or other disturbances, there is no mechanism for soil rejuvenation. Peatland and scrub forests of shore pine expanded across Pleasant Island beginning at about 7,000 BP (Hansen and Engstrom 1996).

The extremely gradual transition from forest to peatland is called "paludification." In the view of proponents of the paludification hypothesis, scrub forest might therefore be seen as a step in the succession from tall-tree forest toward *Sphagnum* bog.

PONDS, MARSH, AND WET MEADOW

Wetlands undergo succession just as forests do, but the process is less apparent to the casual observer. Rather than estimating community age by the quantity of dead wood or the number of rings in stumps, ecologists measure the age of wetlands by the depth of accumulated peat, and with technologies such as radiocarbon dating.

The most classic example of natural disturbance in Southeast is wetland succession near a receding glacier. Just as forest ecologists can examine forests of increasing age at greater distance from the ice face, wetland ecologists have a textbook-clear sequence of
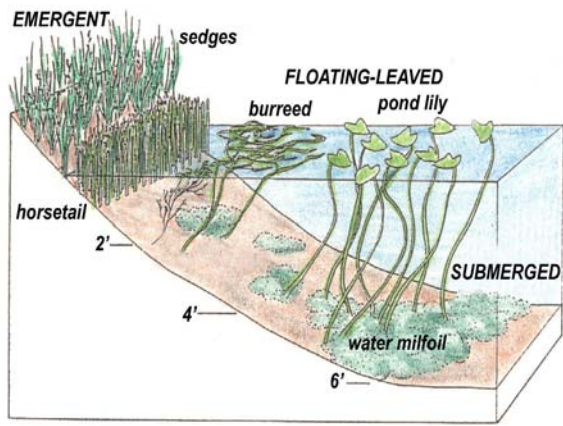
FIG 85 Zonation of aquatic plants on margins of ponds and lakes.

FIG 86 Adult male western toad (*Bufo boreas*) on the edge of a beaver marsh. Once the most abundant vertebrates in wetland habitats throughout Southeast toads appear to have declined precipitously since the 1980s.

FIG 87 Young wetland associated with upwelling along side channel of Taku River near the Canadian border. Hundreds of western toad larvae were swimming in the deepest water in the foreground of the photo, June 25, 2003.

maturing marshes and wet meadows laid out in the intermorainal swales on a transect down-valley.

On these mucky, poorly drained surfaces and in the shallow margins of ponds, the first post-glacial colonists are plants like horsetails (*Equisetum* spp.) and marsh five-finger (*Potentilla palustris*) (Fig 85). Seeds of aquatic plants are efficiently distributed from pond to pond on the feet and plumage of dabbling ducks and shorebirds that visit even the youngest and most barren post-glacial ponds.

At ponds farthest from the receding ice, about 2 centuries after deglaciation, sphagnum mosses (*Sphagnum* spp.) form a soggy margin. Damp meadows and lakeshores of this age may superficially resemble the ancient bogs and fens on surfaces remote from Little Ice Age glaciers. But a poke through the moss with a stick quickly reveals the absence of peat accumulation; these young wetlands rest directly on glacial and palustrine sediments. Soil formation is better measured in millennia than in centuries.

Because of the importance of anadromous fish to the Southeast economy, the streams, rivers, and lakes of the region have been well studied. But the ecology of small, shallow ponds and their associated wetlands in Southeast, particularly those lacking connections to perennial streams, has received almost no scientific attention.

In a study of amphibian breeding habitat near Juneau (Carstensen et al. 2003), pond morphology and diversity were described according to geomorphic origin type. Young ponds and wetlands originated from disturbance by humans, glaciers, glacial rebound (ponds on raised tideland), and beaver. Ancient ponds have developed on bogs and fens and in bedrock depressions. All pond types except those in acidic sphagnum bogs appear to be important to breeding amphibians such as western toad (*Bufo boreas*) (Fig 86) and rough-skinned newt (*Taricha granulosa*).

The ideal breeding pond for western toad—once the most abundant amphibian in Southeast—has shallow, rapidly warmed margins; moderate to high pH; a deeper hole for larval refuge in times of lower water levels; extensive cover of emergent, floating-leaved or submerged aquatic plants; and no surface stream connection (Carstensen et al. 2003) (Fig 87). Western toads have undergone perhaps the most

FIG 88 On some color-infrared aerial photography it is easy to pick out the extremes in bog versus fen habitats. This is a 1979 NASA photo of northern Douglas Island and the south edge of Juneau's Mendenhall Wetlands. Acidic sphagnum bog has a greenish tint in this imagery. Richer fen vegetation is peach-colored. A mottled area with mixed green and peach tints has been labeled "bog/fen/mix."
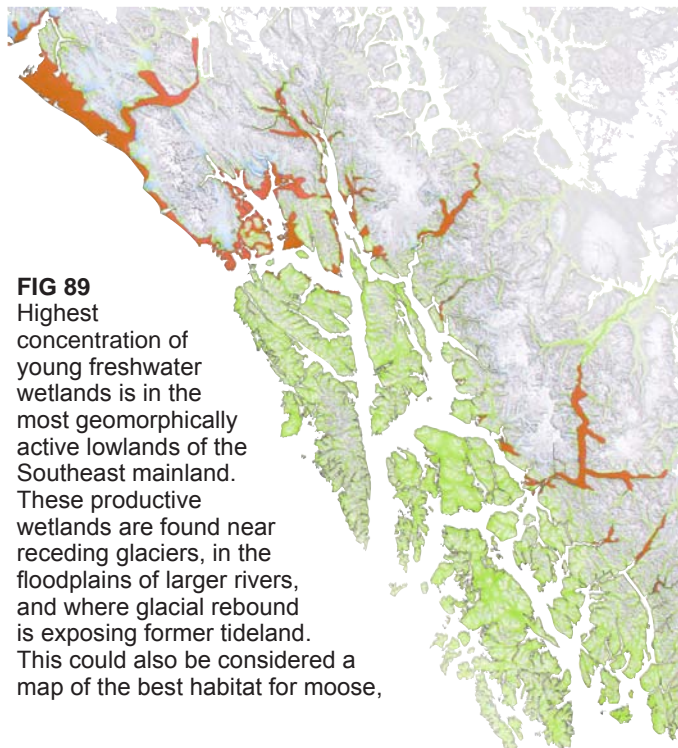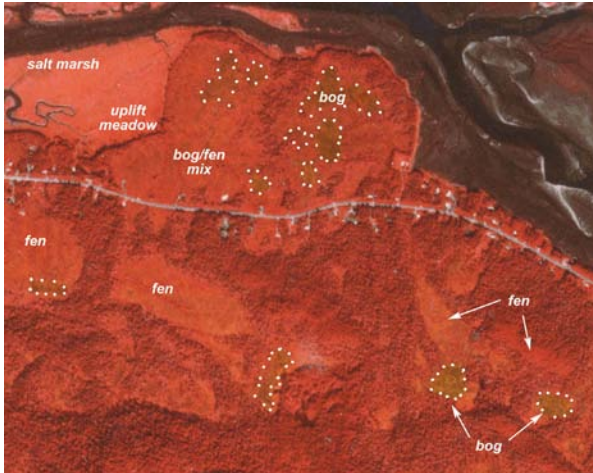
FIG 89 Highest concentration of young freshwater wetlands is in the most geomorphically active lowlands of the Southeast mainland. These productive wetlands are found near receding glaciers, in the floodplains of larger rivers, and where glacial rebound is exposing former tideland. This could also be considered a map of the best habitat for moose,

serious decline of any animal or plant population in Southeast. The cause (or causes) of the decline has not been determined, however.

Considered regionwide, young freshwater ponds and wetlands are most common in the geomorphically active parts of Southeast (Fig 89), including areas near glaciers and along larger rivers and uplifting shorelines. These productive wetland habitats are extremely important to foraging moose and the large numbers of dabbling ducks (species feeding in shallows) that pass through Southeast in migration. Smaller populations of breeding dabblers—primarily mallards (*Anas platyrhynchos*) and green-winged teal (*A. crecca*)—remain to raise their broods here.

Away from such places—for example, on most of the islands of the Alexander Archipelago—Southeast wetlands are generally older and less dynamic. The exceptions are beaver ponds and their associated swampy backwaters. Because beaver are typically a boom-and-bust species, the cycle of dam abandonment and reconstruction leads to perennially rejuvenated wetlands that are some of the best island habitats for the above-mentioned dabblers and amphibians, as well as favored summer grazing sites for deer and bear.

SEDGE FEN

In Southeast, open, spongy wetland with deep peat is usually referred to as muskeg. A better general term

long-used by ecologists for peat-covered terrain with at least 16 inches (40 cm) of organic matter is peatland. If the peatland is dominated by sphagnum moss, it is called a bog (described below). Where lusher vegetation like sedges predominates, the peatland is called a fen.

Although peatland of intermediate character is sometimes difficult to pigeonhole into the category of bog or fen, the extremes in the spectrum are easy to recognize. Compare ground views in Figure 94 to the aerial perspective in Figure 95.

Both bogs and fens are defined by deep, undecomposed peat deposits accumulated over millennia, but fen peat is composed primarily of sedges (*Carex* spp.). Fen plants like deer cabbage and skunk cabbage are less toxic and more palatable than bog plants to grazers like bear (Fig 92) and deer (Fig 90). Oddly, fen sedges themselves appear to be little used by deer and brown bear. Wildlife habitat mapping on the "ABCs" (Admiralty, Baranof and Chichagof islands) in multiple seasons has documented almost no removal of sedge tips. Most sedge consumption appears to take place in the coastal salt marshes (B. Christensen, Southeast Alaska Wilderness Exploration, Analysis and Discovery, Juneau, AK, personal communication 2005).

Hydrology controls the array of vegetative communities developing on peatland. Fens tend to occur on gently sloping surfaces such as the ancient raised marine terraces encompassing Douglas and

FIG 90 Sitka black-tailed buck during summer in rich fen on Kupreanof Island. Foraging values for herbivores are much higher in sedge fens than in sphagnum bogs.

FIG 91 Calcareous fen, Freshwater Creek, Chichagof Island. Road construction impacts groundwater movement into and exiting from these regionally rare wetlands.

FIG 92 Bear diggings for skunk cabbage at border of fen with scrub forest, Port Stewart, Cleveland Penninsula.

Admiralty islands. Fens are enriched by oxygenated, mineral-bearing groundwater from upslope areas, and bogs, which are hydrologically isolated from such "donor" slopes, receive their water from rain or snowfall. Compared to bogs, fens are somewhat less acidic and their groundwater is more mobile. Because of somewhat higher oxygen levels than in bogs, sedge peat is usually more decomposed than sphagnum peat, and therefore stores less water. Wetland ecologists speak of rich fens and poor fens; the latter are less productive and could be considered hybrids between fen and bog conditions. In a successional sense, some of these poor fens may be on a very long trajectory toward sphagnum bog.

Fens present challenges to construction of roads that tend to disrupt groundwater movement. They generally support valuable salmonid rearing streams and require oversized structures for fish passage that entail high maintenance costs (Shepard et al. 1999).

Calcareous fens occur near carbonate bedrock (Fig 91). They are highly productive peatlands with neutral to basic pH and high calcium and specific conductivity (McClellan et al. 2003). Calcareous fens have distinctive flora such as orchids (*Platanthera* spp.*, Malaxis brachypoda*), shooting stars (*Dodecatheon jeffreyi*), and felwort (*Swertia perennis*). Regionally rare calcicoles like mountain bladder fern (*Cystoperis montana*) are found in these fens (McClellan et al. 2003).

Because karst itself is well-drained and rarely supports wetlands, calcareous fens usually develop downslope from karst hillsides, where bedrock shifts to noncarbonate types (McClellan et al. 2003). Groundwater flowing off the carbonate rocks brings nutrients and less acidic conditions than normally found in Southeast peatlands. Calcareous fen habitats are uncommon and inadequately surveyed in Southeast. They may be affected by road building and by logging of karst forests upslope (Shepard et al. 1999).

SPHAGNUM BOG

Bogs occupy surfaces that are poorly drained and level or gently undulating. Bog surfaces are

FIG 93 Common bog plants. Clockwise from upper left: labrador tea (*Ledum groenlandicum*); great sundew (*Drosera anglica*); cloudberry (*Rubus chamaemorus*); bog blueberry (*Vaccinium uliginosum*).

FIG 94 Comparison of bog and fen. *Above*: pond in bog with stunted shore pines (*Pinus contorta*) north of Juneau. The reddish moss is *Sphagnum magellanicum*.*Below*: rich fen on Admiralty Island. Buckbean (*Menyanthes trifoliata*) is emergent in the pond, where rough-skinned newts (*Taricha granulosa*) were swimming.

sometimes raised slightly above those of surrounding forested habitats. Especially abundant on the low-lying islands like Kupreanof and northern Mitkof, bogs are also scattered in smaller amounts throughout Southeast. Unlike in fens, groundwater movement is minimal in bogs. Plant nutrients are in low supply, and bog water is oxygen-starved and often more acidic than that of fens.

Subtle differences in groundwater movements often result in a complex interspersion of sphagnum bog, sedge fen, and less easily defined hybrids of these peatland types. Because bogs and fens have distinctively different wildlife values, accurate wetland mapping is important to land managers. Unfortunately, distinctions between bog and fen are not always as clear as in the color-infrared example in Figure 87. Color signatures shift, even from photograph to photograph in the same flight line. NWI mapping was done by photointerpretation, and only picked out a few extreme types. Additional ground-truthing is always necessary for project-level decisions.

Much of what is known about the post-glacial history of Southeast is owed to the science of palynology. By extracting deep peat cores from sphagnum bogs, palynologists sample the evidence of vegetation (spores, leaf fragments, and other plant components) at successive millennia into the past.

Bog plants grow slowly in the saturated, nutrient-starved environment. Stunted shore pines (Fig 82) no taller than a person can be a century old. Such slow growth cannot support grazing or browsing pressure, and most bog plants are defended from herbivores by toxins. Unlike the robust, waist-high sedges in rich fens, bog species like spikerush (*Trichophorum caespitusum*) and the few-flowered sedge (*Carex pauciflora*) are thin-leaved and inconspicuous. The tender-leaved herbs of fens are replaced in bogs mostly by woody-stemmed dwarf-shrubs like bog laurel (*Kalmia microphylla*) and Labrador tea (*Ledum groenlandicum*) (Fig 93). Most have tough, leathery, evergreen leaves.

FIG 95 Aerial perspective on the bog/fen distinction. Highland plateau south of Chaik Bay, Admiralty Island. Better GIS mapping of this important distinction is a high conservation priority.

FIG 96 Mating bluets (*Enallagma sp.*) on pond lily leaf in small bog pond. Invertebrates of bogs and fens are poorly known in Southeast (But see Hudson & Armstrong [2005] for dragonflies).

FIG 97 Peatland soils are fragile and unable to soon recover from scars such as these 4-wheeler tracks through a bog near Juneau. ORV use in wetlands is a controversial issue in places like Kruzof and Chichagof Islands.

Because of scant vegetation, although bogs may provide well-used travel corridors for large mammals, they do not feed grazers or browsers. The one thing they offer to vertebrate herbivores is delicious berries. Berries such as bog blueberry and cloudberry (*Rubus chamaemorus*) (Fig 93) are among the most distinctively flavored fruits in Southeast. However, by comparison with habitats like the thickets of devil's club, salmonberry, and stink currant in slide chutes and on stream banks, the production of bog berries is relatively low. Few vertebrate species display a preference for sphagnum bog habitat. The greater yellowlegs (*Tringa melanoleuca*)—one of the few shorebirds to breed in Southeast—places its ground nest on sphagnum bogs, where the well-camouflaged female is nearly impossible to detect when incubating. But rather than foraging near the nest, parents commute to other more productive wetland habitats.

As with mammals and birds, amphibians appear to find acidic bog environments less suitable than fens for breeding and rearing (Carstensen et al. 2003). Many invertebrates likely are specially adapted to the unique bog habitats of Southeast, but with the exception of dragonflies (Hudson and Armstrong 2005), these species have not been surveyed.

Implications for Conservation of Terrestrial Habitats in Southeast Alaska

OLD-GROWTH FOREST

Large-tree, old-growth forest types are the most rare forest types in Southeast, comprising only 2.7% of the region (Chapter 2, Table 2). Yet these types have also been the focus of a century of logging in Southeast, and their disproportionate harvest (Chapter 2, Table 3) is arguably the central terrestrial conservation issue in Southeast; many other conservation issues—such as potential long-term degradation of salmon streams—stem from it. Chapters 2, 3 and 4 of this assessment provide a conservative estimate of the extent to which these unique forest types have been logged—province by province—since 1986. Because timber harvest prior to 1986 was highly targeted toward large-tree stands, the quantification in this assessment is a significant underestimate of the actual extent of impact on these rare forest types.

Riverside flood plains and alluvial fans are optimal environments for large-tree forest; however, there is scarcely a coastal alluvial fan remaining in Southeast that has not been logged to some degree—be it handlogged or clearcut. In the 1950s through the 1970s, early clearcut logging throughout Southeast targeted the large-tree stands of alluvial bottomlands and karst (Chapter 2, Table 4). Clearcuts were sometimes very large. Because the largest trees often


FIG 98 Long Bay in Tenakee Inlet, East Chichagof (John Schoen).

grew right beside the streams, forests were typically logged to the banks. With growing concerns over fisheries protection and proportionality, buffer restrictions were instituted in the 1990s. Cutting units also decreased in size, and logging tended to move away from the streamsides onto the upland slopes (Fig 99). This "checkerboard" pattern of logging reduces damage to riparian forests along larger streams but requires more roads that impact smaller tributaries, introduce invasive species, and potentially disrupt wetland functions.

Large-tree karst forests historically received even more logging pressure than did the riparian and alluvial fan forests (Chapter 2, Table 4). As on alluvium, excellent drainage and ease of road-building on low, rolling limestone country hastened the extraction of the karst large-tree forest. The great karst islands of Sea Otter Sound and adjacent northern Prince of Wales (the North Prince of Wales–Kuiu Carbonates ecological subsection) saw the highest percentage of landscape logged of any subsection in the Tongass National Forest, and road density here is also highest (Nowacki et al. 2001).

While stream buffers protected the remaining riparian forest, no similar constraints have been placed upon the logging of
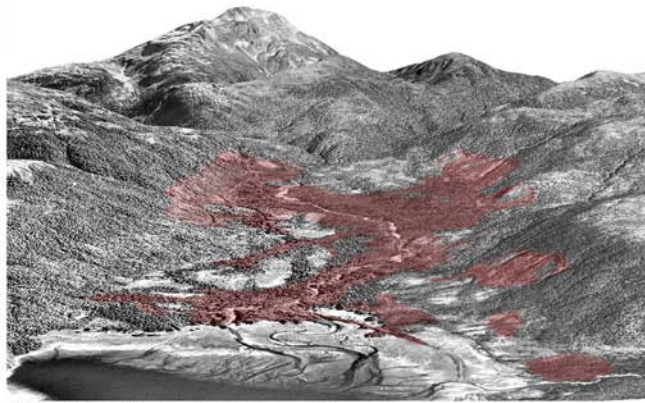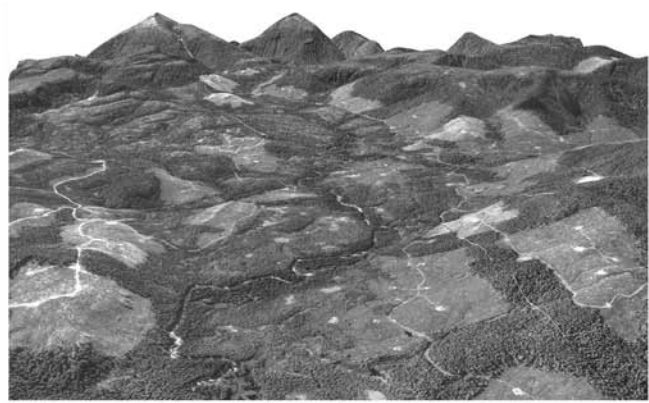
FIG 99 Patterns of logging in Southeast Alaska. Terrain models generated in ArcScene by "draping" 1996 orthophotos over digital elevation models. Vertical exaggeration 1.5x. A) Prior to riparian buffer protections instituted in the 1990s, logging primarily targeted the big-tree bottomland spruce forest. In 1918 a few patches were cut by handsaw near the Fish Bay estuary. Between 1951 and 1967, chainsaws cut all of the great riparian spruce stands right to the stream bank. Brown tint shows extent of this alluvial and toe-slope logging. B) Recent "checkerboard" logging on Forest Service land. Productive upland hemlock-spruce forest logged between 1979 and 1993. Unit sizes 60 to 120 acres (24-49 ha). Stream buffer protected big-tree stands on Kadake Creek in foreground. C) In the late 1980s and early 1990s, SheeAtika Corporation lands on northwestern Admiralty were logged from their property borders down to the lake and stream edges. D) Klukwan Inc. lands on the extraordinarily productive karst forest of Long Island were 85% logged, leaving only sub-commercial patches. The northern half of this island is mostly rolling, low-elevation karst that once supported Alaska's most magnificent big-tree forest. Thousands of acres of giant trees grew here, some to 16 ft (5 m) in diameter.

large-tree karst forest. Karst protections in the TLMP Standards and Guidelines are oriented to "high-vulnerability" cave and landform protection, not the large-tree forest per se. Known cave entrances are protected with narrow forested buffers, but like stream buffers, many of these have blown down (P. Smith, Tongass Caves Project, Whale Pass, AK, personal communication 2005). While the large-tree spruce forest on karst has been almost completely logged, very large hemlocks and cedar remain on karst substrates, and these forest types continue to be logged despite their rarity (Carstensen and Christensen 2005).

In the 1980s, Native corporations selected the best remaining large-tree karst from the Tongass National Forest and logged them, unhampered by the restrictions then placed on federal lands (Fig 99). All karst forest was essentially eliminated from private lands near Hoonah, Kake, Klawock, Craig, Hydaburg, and Ketchikan. The corporations at Klukwan and Angoon, lacking large-tree karst forests in their own traditional use areas, selected the finest karst stands on far-away Long Island and Chasina Peninsula, respectively. The last of the corporation karst forests is now being logged on Dall Island.

Although karst once grew the greatest forests of Alaska, the karst substrate is unpredictably fragile. In some cases, karst has been unable to regrow productive forests after logging because of the subsequent loss of soil into subterranean fissures.

Elsewhere, karst second-growth forests are growing at exceptional rates for Southeast, but this regrowth may not be sustainable through future rotations. According to the 1997 Tongass Land Management Plan, repeated karst logging throughout the world "has led to serious, long-term declines in soil depth and fertility, in some cases resulting in permanent deforestation." (USFS 1997)

Poor and inconsistent records have been kept of the quality of forest cut, both on federal and private lands. Because the karst large-tree forest was generally the first to be cut, reconstructing its former extent is challenging. The task is not as simple as just overlaying a map of known lowland karst with a map of clearcut logging in GIS. For one thing, all lowland karst is not equal in potential to grow large trees. For another, small isolated patches of karst—logged and unlogged—remain unmapped. And even the "managed stands" layer for clearcuts in the USFS GIS database does not map all early cuts that are now hard to detect on aerial photographs. Early selective logging along coastlines and streams is completely unmapped.

Hundreds of acres of lowland karst once held forests superior to the highest-ranking Landmark Trees acre (also a karst forest) of today. Today's number-1 living Landmark Trees stand would not have made the top 1,000 stands in 1950, before industrial-scale logging began. A specific conservation strategy is imperative for this most diminished large-tree forest type.

Extensive logging of large-tree upland hemlock old-growth began after the large-tree spruce forest on alluvium and karst was mostly exhausted, because commercial values are lower in hemlock-dominated
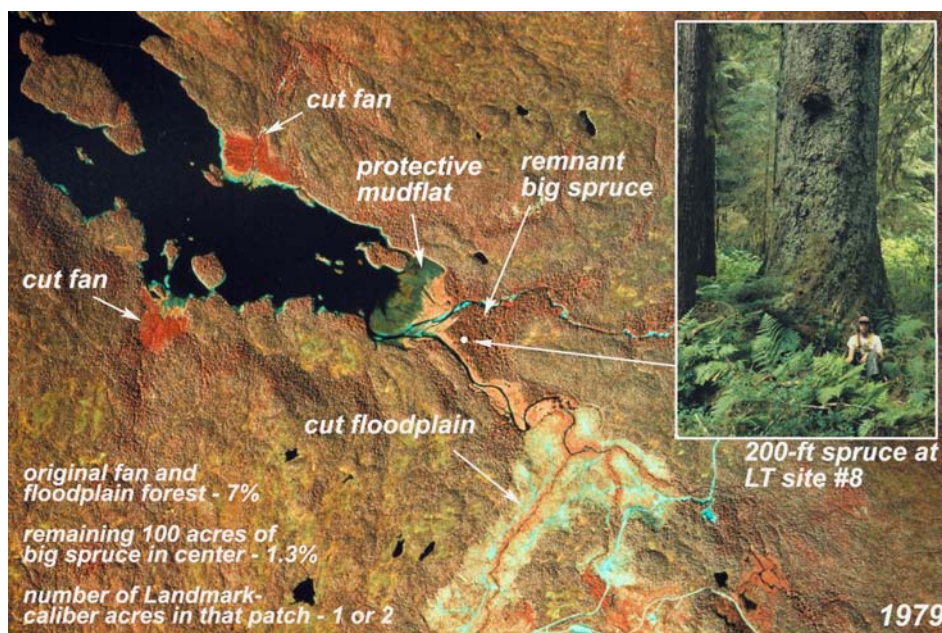
FIG 100 Trocadero Bay, Prince of Wales Island, 1979.   This color infrared air photo shows a typical logging intensity in fairly low-productive watersheds. (Productive lands are usually cut more heavily.) Trocadero's gentle hills still have unlogged scrubby forest. Originally the fan/flood plain big-tree forest occupied 7% of this scene. The 100-acre (40 ha) patch of remnant big spruce at center now comprises 1.3%. Of that, only 1 or 2 acres (<1 ha) are of outstanding Landmark caliber.

Surviving bay-head stands of big alluvial spruces such as this one in Trocadero are very uncommon. This stand was not logged because of the extensive mudflat out in front of it. The broad flats made it impossible for early loggers to bring barge-mounted steam or diesel donkeys close enough to the big-tree stand for yarding.

forest. This forest type reaches its best development on wind-protected lee slopes. Upland hemlock old growth is ill-suited to clearcut logging and the associated dense network of roads. In these slow-growing communities, large trees are attained at the investment of many centuries. Soils are compacted, leached, and rarely churned by uprooting. Especially on slopes, it is difficult to gain access to these stands without eroding the soils and altering surface and groundwater flows. Prolonged regeneration times require long rotation intervals. By comparison, the less compact, churned soils of younger blowdown forests on exposed slopes promote much faster regrowth; these forests more frequently undergo stand-replacing disturbances. Currently, however, proposed cutting units favor multi-aged stands with an abundance of very old trees rather than even-aged post-blowdown forest (Carstensen and Christiansen 2006).

Old-growth redcedar and yellow-cedar provide Alaska's most valuable timber, as cedar forests make up for their relatively low timber quantity with

FIG 101. Rare, large-tree old-growth habitat in the Sitka Sound area, West Baranof Province (John Schoen)

very high wood quality. However, virtually nothing is known about the ecological relationships of cedar forests in Southeast or the biodiversity or wildlife values they harbor. Forest management in Southeast has not yet addressed the long-term sustainability of this forest type, and no TLMP Standards and Guidelines have been implemented to avoid disproportionate harvest of this unique forest type. In light of the extensive die-off of yellow-cedar and of the attractiveness of the cedars in the timber market, it is important to quickly develop a cedar-forest conservation policy if these ancient trees and their associated biodiversity are to be sustained.

In the case of greatly diminished large-tree forest types, such as alluvial and karst forests, restoration in addition to protection is necessary to maintain biological diversity in a number of biogeographic provinces, particularly along anadromous streams that have lost their longterm supply of massive logs and channel-margin root structure. The USFS and other land managers in the region are now exploring thinning of riparian second-growth stands within protective stream buffers, not for timber yield, but for fish and wildlife enhancement.

Global climate change is another source of potential concern for the terrestrial habitats of

Southeast. Die-off in the yellow-cedar forests may be attributed, in part, to climate change. As climate warms, timberlines will rise throughout the world. But this effect will be especially pronounced along the northern Pacific coast where timber lines are controlled not so much by temperatures as by heavy, long-lasting snow pack (Alaback and McClellan 1993). Global warming will also cause glacial retreat, not only at the snouts of lowland glaciers, but in mountainous cirques, where new terrain will be exposed to colonization by alpine plants. On other summits with limited acreage of alpine tundra, rare endemic species or subspecies may be "pinched off" by invasion of conifer, shrub, or subalpine meadow vegetation. All of these climate-driven changes will affect wildlife habitat. Studies are needed to better anticipate when and where bottlenecks may occur for species at risk.

MOUNTAIN ZONES

People so far have a limited footprint on mountain environments in Southeast. But those impacts have increased substantially in recent decades, especially with the growth in tourism in Southeast. A new aerial tramway on Mount Roberts above downtown Juneau brings hundreds of tourists per day into subalpine

FIG 102 Wetland mosaic along the Chilkat River in the Chilkat Province. (John Schoen)

meadows and alpine tundra. These habitats are very slow to recover from trampling disturbances. Increased helicopter landings on mountain ridges have an unknown effect on wildlife and vegetation. Examples needing further study are displacement of mountain goats by helicopter traffic and introduction of invasive species through boots and clothing of globe-trotting visitors.

Some level of increased recreation and tourism can probably be accommodated without major conservation impacts, but precautionary management should apply in order to prevent widespread impacts to this fragile habitat in the future.

POORLY DRAINED HABITATS

Forest communities receive more attention in this report than do wetlands because of the widely recognized conservation issues surrounding forestry in Southeast. It should be noted, however, that while a logged forest eventually recovers (maybe after as long as 400 years in Southeast), a filled-in peatland is gone forever, at least during any time scale a human can appreciate. Anthropogenic impacts to freshwater wetlands in Southeast tend to be concentrated around cities and villages. In the places known best—backyards of Southeast residents—these impacts may be even more profound than those affecting forest habitats.

While relatively little timber extraction occurs currently from wet, small-tree forest in Southeast

this habitat consistently faces development pressures on the outskirts of human populations. In almost every Southeast community, the best-drained building sites are already occupied, and additional roads, housing, airports, ball fields, and other developments are forced onto lands with suboptimal drainage.

Especially in Southeast's larger communities, forested and non-forested wetlands are impacted by development. In addition to complete loss of wetlands from fill, road construction blocks groundwater flow, altering wetland hydrologic function and eventually species composition. In the late 1980s, the City and Borough of Juneau commissioned ecologist Paul Adamus to conduct a ranking of surrounding wetlands according to their hydrologic and wildlife values (Adamus 1987). The ultimate purpose of the study was to identify the least strategically critical of these wetlands and open them up to development.

Southeast Alaska encompasses thousands of acres of ancient peatlands: guardians of watershed stability, wellsprings of biodiversity, and libraries of information about past climates and community succession. Heavy losses of wetlands to development in the lower 48 have led to laws that attempt to stem further losses. To some degree such legislation has helped in Southeast; however, an examination of historical aerial photograph sequences for any city or village in Southeast reveals inexorable encroachment. There is still time to learn from mistakes made elsewhere, and to be responsible stewards for *all* Southeast terrestrial habitats.