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A geographical-ecological model for landscape conservation: Development in Western Samoa

Pearsall, Sam Haff, III, Ph.D.

University of Hawaii, 1993

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A GEOGRAPHICAL — ECOLOGICAL MODEL
FOR LANDSCAPE CONSERVATION
IN WESTERN SAMOA

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF HAWAI’I IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN

GEOGRAPHY

MAY 1993

BY

Sam H. Pearsall III

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Clifford Smith
THIS DISSERTATION IS DEDICATED to Linda and Paul Pearsall, my comrades in arms; to my parents and parents-in-law, patient and glad; to Paul Davis, dear friend; and to Dr. Robert Jenkins, Jr. who was the first scientist to apply many of the ecological and geographical principles herein to the challenge of systematically conserving biological diversity.
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and especially, Dr. Art Whistler!
ABSTRACT

The Theory of Landscape Ecology holds that the biological and material interactions among ecosystems are highly (often mainly) influenced by their relationships in geographical space. A conservation corollary states that measuring, modelling, and preserving these spatial relationships provides a useful, approximating approach to conserving the interactions among the ecosystems (ecotopes) of landscapes, potentially resulting in the maintenance of an ecologically stable or meta-stable landscape. The latter can be defined as a landscape where the patterns and processes of component ecosystem interaction are changing relatively slowly and where entropy gradients are shallow. In an ecologically stable or meta-stable landscape, component ecosystems will persist without simplification or collapse, and the ordinary processes of material and biological interaction among ecosystems will not change rapidly.

Networks of nature reserves, corridors, and buffers were designed for the maintenance of ecologically meta-stable landscapes on the islands of Savai’i and ‘Upolu in Western Samoa. The approach involved generating a new map of the vegetation of Western Samoa and the incorporation of these and other data in a geographic information system in order to facilitate cartographic modelling. Intermediate products included maps of the landtypes, the normative vegetation, and the normative ecosystems of Western Samoa. Ecosystem priorities for conservation were selected on the basis of new indices of rarity and threat.
The networks were developed using a rule-based decision model for relatively rare ecosystem types and using a graphical solution for more common types. The rules required the inclusion of all occurrences of the rarest ecosystems and inclusion of all occurrences for moderately rare ecosystems with the exclusion of primary agricultural land in customary tenure. The graphical solution for common ecosystem types emphasized the development of high quality corridors. Finally, buffers were defined around the network cores. The networks were verified, and the process used to generate them was generalized as the Regional Ecosystem Analysis and Landscape Conservation (REAL Conservation) methodology.
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CHAPTER 1

INTRODUCTION: GEOGRAPHIC AND SCIENTIFIC FOUNDATIONS

1.1 The Problem

The challenge of conserving nature is not adequately addressed by the contemporary disciplines of biology and ecology. Geography, with its tools for spatial modelling and analysis and its broad requirement for an understanding of scale, offers an opportunity to address this challenge from a different, complementary perspective. In this paper, the problem is to determine the utility of spatial modelling and analyses for selecting and designing systems of nature reserves on tropical forested islands, and by implication, in other environments as well.

1.2 An Overview of the Thesis

The remainder of this chapter provides geographical and ecological background for Western Samoa, the context for this research, and an overview of the various sciences and their potential contributions to nature conservation at the level of the landscape and on oceanic islands. Chapter 2 provides a review of methodologies available in these disciplines and common to the parent disciplines of geography and ecology. Special attention is paid to the problems of ecosystem (ecotope and landscape) conservation on islands. Chapter 3 describes the process of collecting foundation data, especially on vegetation, and its mapping and assimilation into a geographic information system. Chapter 4 features definition of the ecotopes of
Western Samoa, mapping of their normative distributions, and determination of their rarity and threatened status and their consequent priorities for conservation. The chapter concludes with the synthesis of conservation priorities for the two islands of Savai'i and 'Upolu. Chapter 5 covers the development of conservation networks using rule-based decision models and a graphical solution and then describes the resultant networks. Finally, the networks and the process are generalized. Evaluation and conclusions appear in Chapter 6.

1.3 Western Samoa: The Geographic Context

Western Samoa was selected for this research because it offers considerable biological and ecological diversity in a small tropical island nation (see Figures 1-4) and local endemism is relatively high (e.g., Dahl 1980).

1.3.1 Physical Geography

1.3.1.1 Location and General Description

Western Samoa is a tropical island state with a terrestrial surface of approximately 2,930 km² on two large and several very small islands. These include the inhabited islands of Savai’i (approximately 1,820 km²), 'Upolu (approximately 1,100 km²), Apolima (approximately 2 km²), and Manono (approximately 5 km²).

---

Figure 1. Samoa's Place in the Pacific Ocean
Figure 2. Western Samoa
Figure 3. Savai'i Base Map with Roads
Figure 4. 'Upolu Base Map with Roads
Apolima lies in the Apolima Strait between Savai'i to the west and 'Upolu to the east. Manono is included within the reef on the western end of 'Upolu. Several additional very small, unoccupied islands lie within or on the reef systems of 'Upolu and Savai'i. The most significant of these are Fanuatapu, Namu'a, Nu'utele, Nu'ulua (the Aleipata Islands east of 'Upolu), and Nu'usafe'e (south of 'Upolu). The geographic center of Western Samoa is at 13° 30' south latitude and 173° west longitude. The north to south latitude extent is 11° - 16° south and the west to east longitude extent is 174° 30' - 171° west. Western Samoa’s Exclusive Economic Zone is approximately 131,000 km². Adjacent countries are Tokelau, American Samoa, Tonga, and Wallis and Futuna. Maximum elevations are 1,858 m on Savai'i, 1,100 m on 'Upolu, 200 m on Nu'utele, 165 m on Apolima, and 60 m on Manono, and near sea-level on the smallest islands.

1.3.1.2 Biogeographic Regions

Udvardy lists Western Samoa as part of the Central Polynesian biogeographical (primarily zoogeographical) province (Udvardy 1975, 1984). Takhtajan (1986) includes the archipelago in his Fijian floristic region. Dahl (1980) includes Western Samoa in the South Pacific biogeographic province that includes only Western and American Samoa (excluding Swain’s Island) and Wallis and Futuna.
1.3.1.3 Climate

The climate is generally tropical and mild, having wet and dry seasons. The southern and eastern sides of the main islands tend to receive more rainfall than the western and northern sides due to prevailing southeasterly trade winds and orographic effects (Kear and Wood 1959, 1962; Wright 1963). In Apia, on the northern coast of 'Upolu, rainfall averages 2,870 mm/year with the heaviest rainfall in January (424 mm) and the lightest in July (96 mm) (Taylor 1973). On the windward south and southeastern shores, annual rainfall averages between 5,000 and 7,000 mm (Douglas and Douglas 1989). Rainfall averages 5,000 mm at 1,000 m elevation and 7,000 mm above 1,200 m on Savai’i (Paine 1989). There are no abrupt rainfall transitions; wet and dry seasons grade into each other (Taylor 1973). Droughts are common (Curry 1955, 1962). The mean annual temperature in Apia is 26° C (Cole et al. 1988, Curry 1962).

Major tropical cyclones are rare (Bunge 1984). Minor cyclones struck the country in 1939 and 1966 (Skowron 1987), but on 2 February 1990, Ofa, the worst cyclone in 169 years hit the islands. Wind speeds in Apia were measured at 180 km/hour, and the storm lingered in Western Samoa for most of four days and nights. The north shores of the islands were most seriously affected; the strongest winds came from the north and storm surges were felt as the storm passed just west of Savai’i (Ulafala 1990). Wind speeds at Falealupo on the western tip of Savai’i probably considerably exceeded the measured speeds in Apia. On 8 December 1991,
Western Samoa was struck again by a major tropical cyclone. Cyclone Val was reported by the Australian Overseas Disaster Response Organization to have been even worse than Ofa, and damage was very severe, including the stripping of 90% of all foliage from the forests (Church World Service 1991).

1.3.1.4 Geology, Soils, and Landforms

All of the islands are volcanic in origin and lie near the northern terminus of the Tonga Trench at the subduction juncture of the Pacific and Indo-Australian plates (Jarrard and Clague 1977). There have been six major periods of vulcanism. The earliest began in the Pliocene, and the latest is still considered to be in progress (Kear and Wood 1959, 1962; Trotman 1979). The island of Savai'i is still considered active, with its most recent eruptions producing lava flows between 1905 and 1911 (Douglas 1969; Kear and Wood 1959, 1962). 'Upolu is older, and, as the result of weathering and erosion, generally more rugged with deeper soils and better developed wetlands (Curry 1955; Kear and Wood 1959, 1962; Wright 1962, 1963).

Wright (1962, 1963) describes the soils of Western Samoa. Wright’s work was extensively revised in 1989 and 1990 (ANZDEC Ltd. and DSIR Division of Land and Soil Sciences 1990). That study lists 87 soil series that are classified according to the standard US soil taxonomy (USDA Soil Survey Staff 1975, 1988).
and correlated with Wright and with the FAO and UNESCO classification (UN FAO and UNESCO 1986).

Curry (1955) defines 12 landform regions for Western Samoa. Working in 'O Le Pupu - Pu'e National Park, a United Nations Development Advisory Team described 10 land systems (landform associations) and approximately 20 landforms (Ollier et al. 1979).

In Western Samoa, environmental gradients are quite steep, with cloud forests occupying the upper elevations on Savai'i, montane and mid-elevation rain forests on the larger islands, and coastal and littoral forests on most islands. The coastal ecotopes include rock and sand strand communities, isolated mangrove forests, and extensive fringing reefs. Most of the coastal forests have been replaced by gardens, plantations, villages and, in Apia, urban development (Cameron 1962, Douglas 1969, Thomas 1984).

1.3.2 Biological Diversity and Species at Risk²

Whistler (in press) estimates that Western Samoa supports 775 native vascular plant species of which approximately 30% of the angiosperms are endemic, including the endemic genus Sarcopygme. There are about 280 genera of native

²A complete list of endemic and threatened species is available in the form of a computerized data base (Pearsall 1990b).
angiosperms (more than any other archipelago in Polynesia) (Whistler 1990, 1992).

In addition, there are about 250 introduced plant species. Whistler lists 47 threatened vascular plant species (personal communication 1991; also see IUCN CMC Threatened Plants Data Unit 1987).

There are 21 butterfly species in Western Samoa (Dahl 1986). Western Samoa has 1 species of swallowtail butterfly. It is endemic to the Samoas, and considered to be threatened (Collins and Morris 1985). Only 2 endemic endodontid snails are known from Samoa. This relatively low original diversity (for Polynesia) of endodontid snails is probably attributable to an endemic ant that preys on them. There are 9 endemic charopid snail species and 8 endemic partulid snail species. Introduced ants have caused many local snail extinctions among these groups, and endemic snail species are now restricted to high elevations (Dahl 1986, Kondo 1980, Solem 1976-1982). Approximately 15 (mostly marine) invertebrates are considered threatened in Western Samoa (Dahl 1986, Eaton 1985, Fitter 1986, IUCN CMC and ICBP 1988, IUCN SSC Mollusc Specialist Group 1987, Lewis et al. 1988, Paine 1989, Solem 1976-1982, Wells 1985).

Western Samoa supports 11 species of reptiles (Brown 1957) including 7 species of lizards and 1 snake (Dahl 1986). None of Western Samoa’s terrestrial reptiles is considered threatened, but all marine turtles that visit the islands are considered threatened or endangered on a global basis (Balazs 1982, Eaton 1985, Fitter 1986, Groombridge and Wright 1982, IUCN CMC and ICBP 1988).
Of 43 resident bird species in Western Samoa, eight are endemic (Pratt et al. 1987). Most resident land birds have one or more subspecies endemic to Western Samoa (David Blockstein personal communication). Nine bird species are considered to be threatened (Chambers 1985, Collar and Andrew 1988, Dahl 1986, IUCN CMC and ICBP 1988, KRTA 1988, King et al. 1981, Mountfort and Arlott 1988, Paine 1989, Pratt et al. 1987).

The archipelago supports one sheath-tailed bat and two flying foxes or fruit bats. All three are considered threatened (Burton and Burton 1987; Dahl 1986; IUCN CMC and ICBP 1988; Paine 1989). Six cetaceans (whales and porpoises) that visit Samoa’s waters are considered threatened (Burton and Burton 1987, IUCN CMC and ICBP 1988, Klinowska 1991, Thornback et al. 1978, Townsend 1935).

1.3.3 People and Land in Western Samoa

1.3.3.1 Historical Background

The Samoan Islands were probably first settled by Austronesian speaking, proto-Polynesian people around 3,000 BP (Bellwood 1980, Bunge 1984). Directly or indirectly, these islands were (along with Tonga) very likely the origin of Polynesian voyages which settled the remainder of the Polynesian region from Hawaii to the north, the Marquesas to the east, Easter Island to the southeast, New Zealand to the south, and Polynesian outliers in Melanesia and Micronesia such as Kapingamarangi Atoll to the west (Bellwood 1980). Europeans first settled in Samoa

Important characteristics of post-European Western Samoa are the rapid assimilation of Christianity into the Samoan culture; the willingness and ability of Samoan people to interact flexibly with Europeans in political and economical matters; and the unwillingness of Samoans to abandon Fa’a Samoa (the Samoan way) which includes traditional concepts of village life, political consensus, the authority of chiefs, land tenure, and human relationships with the environments of Samoa (Davidson 1967, Holmes 1974, Meleisea 1987, Ngan-Woo 1985).

Western Samoan relationships with colonial administrators, beginning with the Germans in 1899 and ending with independence from New Zealand in 1962, were rarely relaxed (Bunge 1984, Davidson 1967, Thomas 1984). Western Samoa was the Pacific’s first island state to achieve independence from its colonial masters (Davidson 1967, Meleisea 1987), and the tradition of providing regional leadership is well established and very strong.

1.3.3.2 Land and Authority

In traditional Samoan villages, village affairs are controlled by a fono (council) of ‘aiga (family) Matai (heads or chiefs) (Holmes 1974, Meleisea 1987, Omeara 1987). Since Samoan descent is traced through both parents, most Samoans
can claim relationships with several Matai, but in practice, Samoans feel most closely related to the Matai of the 'aiga with which they reside (Holmes 1971, 1974). In theory, any Samoan can succeed a Matai to whom he or she is related, but in practice, brothers and sons most often are elected to the title. A strong commitment to the welfare of the 'aiga as demonstrated by service is the most critical qualification (Holmes 1971, 1974). In the fono, the Matai’s actions are controlled by the relative rank of his or her title, and according to whether he or she is a Tulafale ("talking chief") or an Ali’i ("high chief") (Holmes 1974). Ali’i have formal power and higher rank. Tulafale are instigators and implementors. Decisions are made by consensus strongly influenced by deference to titular rank (Holmes 1971, Omeara 1987, Runeborg 1980).

Following independence, the Matai were the only Western Samoans who could vote, be elected to the national parliament, be appointed judges to the Land and Titles Court, or hold public office (Crocombe 1971b, Omeara 1987). A referendum held in 1990 resulted in universal adult suffrage, but elected public offices continue to be restricted to Matai.

The Matai has the pule (authority) to allocate the use of the 'aiga’s land (Holmes 1971, 1974; Omeara 1987). This authority includes the ability to grant rights of use, to determine labor obligations, and to receive a share of the income or crops (Holmes 1971, 1974; Omeara 1987; Runeborg 1980). The Matai does not have
the right to alienate the land without the consensus of his 'aiga (Holmes 1971, 1974; Thomas 1984; but see Omeara 1987). Use rights are heritable with approval from the Matai (Holmes 1971, 1974). 'Aiga lands typically include village house lots, gardens, plantation lots, and family reserve sections (typically in taro gardens and swiddens) (Holmes 1974, Runeborg 1980). Family reserve sections usually run in strips from the coast into the mountains (Holmes 1971, Merlin and Juvik 1985). In addition, there are village lands. These are typically firewood and medicine gathering areas, beach landings, reef and lagoon areas, and playing fields, but also include unused lands which may be claimed by the 'aiga by establishment of use (Holmes 1971, Omeara 1987, Thomas 1984). When a piece of land is cleared for use, it becomes appurtenant to a Matai title (Holmes 1974, Omeara 1987, Runeborg 1980). Finally, there are district lands claimed by traditional Samoan district councils (made up of the ranking Matai of the district villages). District lands are high mountain lands used primarily for hunting and gathering (Holmes 1971, 1974).

1.3.3.3 Land Tenure

During the period between first European settlement and the establishment of Samoa as a free and neutral nation for the first time in 1889, much land was alienated from the Samoans by Europeans (Holmes 1971, Meleisea 1987). During the period from 1889 to 1899, alienation of lands was forbidden, and alien land claims were evaluated by a fact-finding tribunal and, if necessary, by the Samoan Supreme Court. A claim was not substantiated unless it had been occupied and
worked for at least 10 years and unless proof of payment (excluding firearms and liquor) could be presented. Most claims were evaluated during this period, so when Germany annexed Western Samoa in 1899, the distinction between customary lands and alienated lands was well established (Holmes 1971, Meleisea 1987). The German administration restricted further alienation, but large tracts of arable lowlands were alienated by the government itself for corporate plantation development (Holmes 1971). A Land and Titles Commission was established to resolve issues of tenure (Meleisea 1987, Runeborg 1980).

The New Zealand administration (from 1919) recognized three classes of land in the Samoa Act of 1921. These were Crown Lands (formerly German estate and government lands), European Lands, and Samoan Lands (non-alienated lands) (Holmes 1971, Tiavolo 1984). The Samoa Act established that title to Samoan Lands was vested in the Crown as trustee in perpetuity (Cole 1986). Samoan Lands could be taken for public purposes (Tiavolo 1984). The Land and Titles Protection Ordinance of 1934 broadened the Crown's ability to manage Samoan lands and re-established the Land and Titles Court to settle disputes regarding land tenure and succession to Matai titles (Cole 1986, Meleisea 1987).

When Western Samoa achieved independence in 1962, its new constitution classified all land as Customary, Freehold, or Public (after the New Zealand classification). Customary Land was no longer held in trust by the government
(Meleisea 1987, Runeborg 1980). Alienation of Customary Land was forbidden with the provision that the new parliament could authorize and regulate licenses and leases of Customary Land, and Customary Land could be taken for public purposes (Cole 1986). Furthermore, all land below the high-water mark was declared Public Land (Cole 1986). The Land and Titles Court was retained (Meleisea 1987, Sesega and Burgess 1984). The Western Samoan Trust Estates Corporation (WSTEC) was created as a quasi-governmental corporation to manage the old German estates lands. In 1965, the Alienation of Customary Land Act was passed by the parliament allowing the Matai to lease Customary Land for economic development purposes with approval from the Ministry of Lands (Meleisea 1987, Sesega and Burgess 1984, Tiavolo 1984). The Alienation of Freehold Land Act of 1972 strictly regulated the alienation of Freehold Lands to non-resident corporations and individuals (Tiavolo 1984). In 1977, an act was passed allowing WSTEC to sell certain of its lands as free-holdings for development (Cole 1986).

Table 1. Twenty Year Land Tenure Trend in Western Samoa (Cole 1986, Holmes 1971)

<table>
<thead>
<tr>
<th>LAND CLASS</th>
<th>1962</th>
<th></th>
<th>1982</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ha</td>
<td>%</td>
<td>ha</td>
<td>%</td>
</tr>
<tr>
<td>PUBLIC (&amp; WSTEC)</td>
<td>34,700</td>
<td>12</td>
<td>44,900</td>
<td>15</td>
</tr>
<tr>
<td>FREEHOLD</td>
<td>16,200</td>
<td>5</td>
<td>21,300</td>
<td>8</td>
</tr>
<tr>
<td>CUSTOMARY</td>
<td>242,600</td>
<td>83</td>
<td>227,300</td>
<td>77</td>
</tr>
</tbody>
</table>
The Land and Titles Court settles disagreements concerning succession to Matai title and pule over land. Court decisions are not subject to appeal. The court is heavily influenced by custom and by the recommendations of the local fono (Sesega and Burgess 1984, Seumanutafa 1984). Historically, the Court did not register Customary Lands per se, but instead registered the Matai titles (Thomas 1984). Leases of Customary Lands could be voluntarily registered (Eaton 1985). Public and Freehold Lands were registered by metes and bounds, on cadastral maps, and by recorded deeds of transfer (Sesega and Burgess 1984, Seumanutafa 1984, Tiavolo 1984). More recently, the Court has begun formal registration of titles to and leases of Customary Lands (Meleisea 1987, Sesega and Burgess 1984, Seumanutafa 1984, Tiavolo 1984).

Modern influences are modifying the relationships between Western Samoans and the land (Holmes 1974). For example, the cash economy is encouraging more independent use of land, and a modified form of land tenure system is emerging de facto allowing Customary Lands to be treated as the private property of the individual (Omeara 1987). Today the Matai often assigns land-use rights to heads of households, and thereafter, exerts virtually no influence over their use of the land, permitting individualized economic effort through the growth and sale of cash crops (Holmes 1971, 1974; Thomas 1984). Similarly, few fono now attempt to regulate the use of village and district lands cleared and brought into use through individual efforts (Holmes 1971, Omeara 1987). Population growth is resulting in village crowding.
People are leaving the coastal villages to build family dwellings in the inland garden plots which they have worked (Cole 1986, Holmes 1971). It also is now common for the Matai to establish and manage plantations on land over which they exercise pule, paying wages to the 'aiga members who work the land (Sesega and Burgess 1984, Seumanutafa 1984). The government and some Matai are leasing timber rights to foreign timber companies, especially on Savai'i (Knibb 1984). Splitting of Matai titles and creation of new Matai titles is resulting in the splitting of 'aiga lands (Holmes 1974, Omeara 1987, Runeborg 1980, Thomas 1984). These trends are producing a category of land which is technically Customary Land but which is highly fragmented, which is sometimes heavily impacted by timber removal, and which is treated as Freehold. This class of land is a source of much insecurity and litigation, as when the Matai attempt to regain control (Omeara 1987, Runeborg 1980, Sesega and Burgess 1984, Seumanutafa 1984, Thomas 1984). Land disputes increase pressure on undeveloped land while sometimes resulting in arable land lying fallow (Runeborg 1980).

1.3.4 **Protected Areas in Western Samoa**

In 1958, the Administration of Western Samoa set aside Robert Louis Stevenson’s tomb site as the Robert Louis Stevenson Memorial Reserve (.5 ha) and an adjoining 52 ha area as the Mt. Vaea Scenic Reserve. The Stevenson family home, Valima, became the Government House, and later, upon independence, the residence
for the head of state (Government of Western Samoa 1985, 1989; Paine 1989; Trotman 1979).

In 1974, Western Samoa passed legislation to provide for the establishment of a National Parks and Reserves System on Public Lands (Eaton 1985; Government of Western Samoa 1985, 1989; IUCN CMC 1985; Paine 1989; Trotman 1979). The act required that National Parks, except for those on uninhabited islands, must include at least 600 ha. Categories for Nature Reserves, Historic Reserves, and Recreation Reserves were also established (IUCN CMC 1985; Paine 1989, 1991). There was, however, little information on which to base the selection of new protected areas. In 1975, at the request of the Government of Western Samoa, a United Nations Development Advisory Team (UNDAT) prepared a plan for *A National Parks System for Western Samoa* (Holloway and Floyd 1975).

In 1978, based on the UNDAT plan, 2857 ha of Public Land on the southern side of 'Upolu were set aside as 'O Le Pupu-Pu’e National Park (Government of Western Samoa 1985, 1989; IUCN CMC and IUCN CNPPA 1985; Paine 1989, 1991; Trotman 1979). The 2800 ha area is twice the size of the original 1975 recommendation. The purposes of the park are to conserve natural features in an unmodified state, to protect water supplies, to provide a resource for environmental education, and to attract tourists (Trotman 1979). 'O Le Pupu-Pu’e extends from mountain top to coast and includes the entire topographic gradient of leeward 'Upolu.
(Ollier et al. 1979, Trotman 1979). The park was established on old lava flows and cinder cones that would provide poor soil for agriculture, so demand for the land was low. A result is that the edaphic diversity of leeward 'Upolū is poorly represented in the park (Merlin and Juvik 1985, Trotman 1979).

The park theoretically is buffered in part by Public Lands (state forest and catchment lands and an experimental demonstration farm) (Eaton 1985, Paine 1989, Trotman 1979). Customary Lands and Public Lands allocated to villages adjoin about one third of the park boundary (Eaton 1985, 1986). Encroachments from wood cutters, swidden gardeners, squatters, and bird hunters are occasional along the lowland boundaries and road (Eaton 1985, IUCN CMC 1985, Merlin and Juvik 1985) and continue to be a problem. Unfortunately, the major encroachments in the park have come in the lower areas of the inland sections by expansion of land-use and land conversion adjacent to the Public Lands and also along the 'O Le Pupu coast where a government radio station has been installed (Pearsall and Whistler 1991b).

In 1978, the Mount Vaea Scenic Reserve (52 ha) and the Robert Louis Stevenson Memorial Reserve (.5 ha) were combined as the Tusitala Historic and Nature Reserve. The Valima Botanical Garden (12 ha) was established on lands adjacent to and formerly belonging to the residence of the head of state, and the Togitogiga Recreation Reserve (2.5 ha) was established adjacent to the administrative headquarters of 'O Le Pupu-Pu'e. Finally, in 1979, the Palolo Deep Marine Reserve
was established on 22.3 ha of submerged reef near Apia (Eaton 1985, 1986; Government of Western Samoa 1985, 1989; IUCN CMC 1985; IUCN CMC and IUCN CNPPA 1985; Paine 1989, 1991). Of these several small reserves, only portions of the Tusitala Reserve play a significant role in the conservation of the terrestrial ecotopes of Western Samoa (Eaton 1985, Government of Western Samoa 1985, Paine 1989).

Several proposals for additional protected areas in Western Samoa have been developed. Beichle and Maelzer (1985), writing for the International Council for Bird Preservation, recommended seven protected areas for forest birds in Western Samoa. Only two of these duplicate the 1975 UNDAT recommendations, and one of these is 'O Le Pupu-Pu'e. Hay's 1986 report on Bird Conservation in the Pacific Islands supported several of the 1975 recommendations. KRTA (1988; Firth and Darby 1992) re-proposed the sites in the Holloway and Floyd 1975 proposal with elaboration of a Mt. Silisili National Park plan to include both major lava flows and several other sites. Chew recommended (1987) that the Aleipata Islands should be established as a marine national park and biosphere reserve. A follow-up feasibility study was prepared by Andrews and Holthus (1989). Based on their terrestrial ecotope research, Pearsall and Whistler (1991a) proposed a system of 26 landscape reserves that would include major regions of rain forest lands and coastal wetlands on Savai'i and 'Upolu as well as all of the Aleipata Islands (also see Pearsall and Whistler 1991b).
The 1974 act requires that protected areas be established on Public Lands (Eaton 1985). The act has since been amended to permit the establishment of protected areas on leased customary lands (Government of Western Samoa 1985). The large majority of the remaining, unprotected lands recommended in the 1975 report (14,200 ha out of 16,100 ha, or 88%) are Customary Lands (Eaton 1985, Government of Western Samoa 1985). The Government of Western Samoa is reluctant to rely on leases of Customary Lands for protected areas. This reluctance is attributable in part to the fact that Customary Land tenure is complex and often contested and in part to the government’s respect for both customary rights and human needs for arable land (Eaton 1985, Merlin and Juvik 1985). The future expansion of Western Samoa’s protected areas system will be dependent on reinforcing customary approaches to land conservation complemented by non-acquisition-based land protection tools (e.g., dedication of Customary Lands) (Eaton 1985, 1986; Government of Western Samoa 1985; Holloway and Floyd 1975).

1.4 The Challenge of Conserving Nature

The conservation of nature is a societal goal in virtually all countries. Even those that cannot generally afford to invest in nature conservation regard the goal as desirable and worthy. Many countries and international agencies now sponsor programs to protect wilderness, to establish parks and reserves, and to conserve biological diversity (IUCN 1980, 1985; Wood 1985).
Public policy in virtually all industrialized countries and in most less-industrialized countries now supports the premise that biological diversity should be conserved, often as the highest priority of nature conservation (Bean 1988). For example, in the South Pacific, all but a few of the 22 countries and territories have laws to this effect, and the principle is incorporated into the constitution of Papua New Guinea (Campbell 1990; Pulea 1984, 1985; Venkatesh et al. 1983).

Although the term "biological diversity" traditionally includes taxa (generally species), ecosystems, and genes (Birch and Cobb 1981), biological diversity conservation has focused mainly on species in danger of becoming globally or locally extinct (Bean 1988). There is, however, a growing global awareness of the essential requirement that, if species and genes are to be conserved, ecosystems must be protected (and vice versa, the three are inseparably and hierarchically linked). In the United States, protection is provided for ecosystems identified as critical habitat for endangered species (Sidle and Bowman 1988), but no public policy has been promulgated on behalf of endangered ecosystems (Caldwell 1970, 1990; Ecosystem Maintenance Panel 1982).

The United Nations Educational, Scientific, and Cultural Organization (UNESCO) Man and the Biosphere Programme (MAB) and the World Conservation Union (IUCN, formerly the International Union for the Conservation of Nature and Natural Resources) encourage the establishment of reserves to protect representative
examples of all ecosystems (typically formations) in each bioregion (Dasmann 1972; Ezcurra 1984; Harrison et al. 1984; Miller 1984; Udvardy 1975, 1984; UNESCO 1974). Austin and Margules (1986) have pointed out that for networks of representative ecosystem reserves to be effective, they must include adequate habitats for viable populations of all of a bioregion’s species. As the result of an initiative from less-developed-country members, the United Nations General Assembly (1985) established a "World Charter for Nature" that calls for the conservation of all species and representative examples of all ecosystems (Wood 1985). Caldwell (1970, 1990) and Schultz (1967) have suggested that it would be logical and desirable to consider the ecosystem (at the scale of the ecotope, discussion below) to be the fundamental management unit for all natural resources.

Many species have very large ranges, and protecting ecosystems at very large scales is not usually feasible. For example, consider the "greater Yellowstone ecosystem" including Yellowstone and Grand Teton National Parks plus six contiguous national forests and two national wildlife refuges as well as other public and private lands. Yellowstone National Park was established in 1872 as one of the world’s first nature reserves, and as its first "national park." At just under 900,000 ha, Yellowstone is the largest American park outside of Alaska, and it ranks among the world’s largest reserves (IUCN CMC and IUCN CNPPA 1985, Ramade 1984). But Yellowstone National Park is not in all ways an effective nature reserve. Newmark (1985) has concluded that the national park is too small to provide adequate
protected habitat for many of the species that live there. Many authors are now arguing that even the greater Yellowstone ecosystem may be inadequate for conservation of wide-ranging species without establishing a coordinated, regional, conservation-oriented, land-use plan (Clark and Zaunbrecher 1987, Power 1991, Romme and Knight 1982).

In the last decade it has become apparent that protected areas alone are insufficient for the conservation of biological diversity (Grumbine 1990, Newmark 1985). Protected areas must be selected, designed, connected, and spatially related so that the landscape itself, including its human systems, provides an adequate environment for the survival of indigenous species and ecosystems (Jenkins 1989, Noss 1987a, Noss and Harris 1986, Pimentel et al. 1992, van Selm 1988, World National Parks Congress 1984). The policy approach to biological conservation must shift from one of segregation of human and "conserved natural" ecosystems to one of integration. Such a landscape would provide a naturally healthier environment for human habitation (Ehrlich and Mooney 1983; Pielke and Avissar 1990; Simmons 1966, 1978, 1979).

Two relatively new disciplines now address the problems of conserving biological diversity. These are a) conservation biology, with its roots in genetics, population biology, and biogeography and b) landscape ecology, deriving mainly from vegetation ecology and the regional and spatial analyses of geography. Conservation
biology has traditionally focused on the problems of designing and adequately managing nature reserves, although this is changing rapidly (e.g., Hall 1987). Landscape ecology has focused on integrated analyses of ecosystems (ecotopes and landscapes). These two disciplines are combined synergistically by practitioners in the emerging professional field(s) of biological and environmental conservation.

1.5 Ecologically Stable Landscapes: Scientific Background

1.5.1 Biological Diversity

Biological diversity has traditionally been defined as the variety of genes, taxa (usually species), and ecosystems in a geographically limited place (Birch and Cobb 1981). Noss (1990) expanded the concept to include landscapes and populations. By including the former, he included ecological and geographical diversity. By including populations, he included within the concept of biological diversity such phenomena as migrations. Only the concept of metapopulations is now missing from what would otherwise be a complete hierarchical order of biological information above the level of atoms and below the level of biomes. McNeal (1986) has argued that the variety of organization of matter developed as the artifact of individual organism interactions with the environment should also be included as pattern diversity (e.g., animal trails and dens in the forest), thus expanding the concept to include ecological events.

Diversity can be simply defined as the number of kinds of things in a geographically limited place (a set), also known as alpha diversity. This is the
traditional concept used in the previous definitions. The diversity concept can be expanded in two other ways. One option is to consider, in addition, diversity along a gradient (beta diversity) or between places (e.g., between ecotopes in the landscape) (gamma diversity) (MacArthur 1965, Walker 1989, Whittaker 1975). The other option is to apply information theory to develop indices of diversity in which diversity is equated with the information (uncertainty or entropy) content of a system. Shannon and Weaver (1949) developed this concept, and MacArthur (1957, 1965) adapted it to the analysis of biological diversity (also see Mueller-Dombois and Ellenburg 1974, pp. 212-230; Walker 1989; and Whittaker 1975, pp. 94-103 for variations). The expansion of the diversity concept to include gradients and between-place-measures requires the use of information-theory-based indices.

Based on the background above, biological diversity can be redefined simply as the information content of an ecosystem (Jenkins 1977). It can be estimated by using traditional measures of information content in single places, along gradients, or between places. Just as different levels of biological systems are distinguished by compositional, structural, and functional characters, so are the components of biological diversity differently measured at different levels. Noss (1990) provides indicator variables and methods for measurement of diversity at each of the levels he recognizes.
1.5.2 Biological Conservation

In 1938, Sauer noted the extirpation and extinction of species caused by humans. He felt that this was a trend that interfered with the natural functioning of landscapes. This was a remarkably prescient observation, for most observations of species decline in those days (e.g., Jackson 1946) were primarily concerned about the loss of species as resources in the landscape (e.g., game species, song birds, sources of medicine). Today, while the conservation of species has become conventional wisdom, the resources perspective is still dominant (McNeely and Miller 1984; Myers 1980; Oldfield 1984; OTA 1987; Prescott-Allen and Prescott-Allen 1982, 1983, 1986).

Other common reasons for conserving biological diversity now include its value for scientific research (previous references), ethical responsibilities to species and/or future human generations (Ehrenfeld 1972, 1986; Hughes 1985; Rolston 1985; Wilson 1984), and ecosystem services (e.g., filtering impurities from water) (Ehrlich and Ehrlich 1981, Ehrlich and Mooney 1983, Westman 1977). Wilson (1985a, 1985b, 1988) provides excellent discussions of the requirement to conserve biological diversity so as not to undermine the processes of evolution.

A few ecologists and geographers have made the argument that species diversity must be conserved so as not to inadvertently undermine the functioning of ecosystems (Ehrlich and Ehrlich 1981; Ramade 1984; Simmons 1966, 1979; Wilson
1985). Recently, this concern has been extrapolated to the conservation of ecosystems themselves so as to conserve the functioning of the landscape (Naveh and Lieberman 1990; Noss 1983 et seq.).

Among the earliest proponents of ecosystem conservation, 14 years before the term "ecosystem" had been coined, and 17 years before Sauer's article, Sumner (1921) wrote on behalf of the Ecological Society of America about the obligations of biologists to conserve natural conditions lest natural systems cease to function. Now it is generally considered that protected areas should be systematically created to conserve biological diversity at least at the levels of ecotopes and species (e.g., IUCN 1978, 1980, 1985; McNeely and Miller; Ratcliffe 1977).

1.5.3 Conservation of Species or Ecosystems?

Ecosystems and species cannot be conserved independently. Ecosystems are comprised of populations of species and their abiotic environments. Species populations rarely survive independently of their ecosystem habitats. Unfortunately, this absence of a dichotomy is not universally acknowledged.

Based on experience in Hawai'i, Scott et al. (1987) proposed to shift the emphasis of nature reserve selection and design from single (threatened or endangered) species conservation to a "multi-species" approach with emphasis on areas of high species richness ("centers of endemism" sensu Diamond 1986), with
somewhat more emphasis on areas with more threatened or endangered species. In
the same article, the authors advocated the use of GIS technology to identify for
protection those vegetation types not currently included in nature reserves. In both
cases, the implication was that too many resources were being expended on individual
endangered species, and attention should be shifted to ecosystems. This resulted in a
debate about whether conservation priority should be given to species or ecosystems
(Roberts 1988; Scott et al. 1989a, 1989b).

In fact, ecosystems are increasingly emphasized over species in the language
of conservation planners. An operational goal has been established by IUCN and the
governments of numerous countries to protect representative examples of all
ecosystem (typically formation) types in each of the earth’s major biological regions
(Austin and Margules 1986; Crumpacker et al. 1988; Dasmann 1972; Harrison et al.
1984; IUCN 1980, 1985; MacKinnon et al. 1986; Margules and Usher 1981; Smith
and Theberge 1986; Udvardy 1975, 1984). However, none of these authors ever
suggests that the goal of conserving ecosystems precludes or excludes the goal of
conserving species. The question is really one of scale, where those operating at
large spatial scales must operate at higher hierarchical levels, or the detail becomes
overwhelming. Austin and Margules (1986) take some pains to emphasize that a
representative set of ecosystems must, by definition, include the full range of species
diversity in the planning region.
To borrow perspective from hierarchy theory (discussed below, O'Neill et al. 1986), ecosystems are the constraining and controlling contexts for populations. The reaction times of ecosystems are slower than those of populations. Thus, while ecosystems are emphasized more broadly (spatially and temporally), species must be monitored and steps taken to address the problems of declining populations, generally by correcting problems at the ecosystem level. The Nature Conservancy has described this as the coarse filter - fine filter approach (Jenkins 1982) to addressing the single problem of conserving biological diversity.

1.5.4 Conserving Landscapes

The last section discussed the perceived conflicts between proponents of species versus ecosystems conservation. It was obvious that ecosystems could not be conserved without conserving their component species, and that species could not be conserved without conserving their ecosystem habitats. Forman (1990b) asked whether landscapes (including ecosystems dominated by human activities) do not require conservation also. He made the point that landscapes, as systems of ecotopes at a higher order of spatial and functional hierarchy, and thus operating at different spatial and temporal scales than ecotopes, have emergent properties that result in the requirement for a different suite of tools for analyses and conservation. He also stated that "a sustainable environment" at the temporal scale of human generations and the spatial scale of the landscape would evidence adaptability and change in the context of a slowly and irregularly shifting but steady-state mosaic of landscape units.
(patches, corridors, etc.) within which more rapid fluctuations can be accommodated (essentially an extrapolation of the within-ecosystem patch dynamic; Foster 1986, Picket and Thompson 1978, Pickett and White 1985, Shugart and West 1981). In fact, it seems very doubtful that true stability can be achieved at any scale smaller than that of the landscape (also see Noss 1987c, Pimentel et al. 1992).

A strong movement has developed within IUCN for the conservation of cultural landscapes. Several national programs have been designed to conserve the scenic quality, biological diversity, and/or traditional social and economic structure of landscapes (IUCN Conservation Monitoring Centre 1987). Most notable among these is the National Park system of the United Kingdom (Poore and Poore 1987). There are also a number of national and international programs designed to conserve representative ecosystems (formations) within biogeographic regions (Austin and Margules 1986, Crumpacker et al. 1988, Harrison et al. 1984). A fortunate side-effect of these programs is that ecological stability of the landscape is often, partially conserved.

1.5.5 Ecosystems are Systems

Systems have been defined as simply as "that part of the environment which is under primary consideration" (Trudgill 1977, p. 11), but they are more generally considered to be structured sets of objects along with their attributes and relationships (Hall and Fagen 1956). Systems are also considered to operate as complex objects
according to some observable pattern (Chorley and Kennedy 1971, pp. 1-2). Systems are characteristically considered to display linkage between form and function, to require inputs and to generate outputs, and usually to have internal mechanisms for responding to inputs (Chorley and Kennedy 1971, pp. 1-22; Trudgill 1977). When inputs to the system are generated by the environment of the system in response to outputs from the system, the system has the characteristic of feedback. When the feedback regulates or controls the system behavior, while the system mediates the feedback, it is said to be a cybernetic system (Shannon 1953).

von Bertalanffy is generally given credit for founding General Systems Theory (first codified in von Bertalanffy 1951; also see Harvey 1969, pp. 447-480). It was this theory, intended as a unifying concept for all scientific endeavor, along with the organismic theory of vegetation succession and climax (Clements 1916, 1936), that inspired Tansley to coin the term "ecosystem" in 1935 for a community of organisms interacting with their physical and biotic environment (Fosberg and Pearsall in press).

The system concept of the ecosystem is not confined to any scale, and natural ecosystems physically exist in a size continuum ranging from the ecosystem in the cup of a bromeliad to the ecosystem of the entire planet, and in a nested-component hierarchy that extends from the organelles in a cell to the biosphere (Evans 1956, Margulis 1981, O'Neil et al. 1986, Schultz 1967, Stoddart 1967, Tansley 1935). The behavior of an ecosystem is determined by the potential behaviors of its
component members and the constraints imposed by the system(s) of which it is a member (O’Neill et al. 1986, 1989), so hierarchical position is partly deterministic.

To give the ecosystem concept utility at the level of local human activities, the term "ecotope" was proposed by Tansley (1939) as the ecosystem of the relatively uniform vegetation stand, also called the "biogeocoenosis" by Sukachev (1950). Planners typically operationalize the concept of ecosystem at the meso-scale of the terrestrial vegetation stand or the aquatic or marine landform (Dourney and McLellan 1984, Maragos et al. 1983, Odum 1969). The result is an operational scale somewhere between tens and thousands of hectares.

Ecosystems are not, however, arbitrary subsets of the environment as some have suggested (e.g., Trudgill 1977, p. 11). Holling states that ecosystems include "communities of organisms in which internal interactions between the organisms determine behavior more than do external biological events. External abiotic events do have a major impact on ecosystems, but are mediated through strong biological interactions within the ecosystems" (Holling 1986).

In other words, in the cloud of possible interactions in the larger ecosystem, the smaller or included ecosystem is the locus of probability (the attractor, to borrow a term from the mathematics of dynamic systems) for a subset of those interactions. In the remainder of this thesis, unless otherwise specified, the term ecosystem is understood to conform to Holling’s meaning. This research focused on ecosystems of
the scale of and coinciding with ecotopes. Ecosystems that are larger than and that contain ecotopes are referred to as landscapes (discussion below).

1.5.6 Ecosystem Concepts: a Modern Perspective

1.5.6.1 Succession and Climax

The concepts of plant succession and vegetation climax were developed in vegetation science by Clements (1916, 1936), and for many years, they figured prominently in ecosystem ecology. "Succession" is the chronological sequence of biota occupying a place; the replacement of one suite of species by another (and so on) as the environment is altered by organisms. "Climax" refers to a condition of equilibrium between the suite of species and the physical environment of an ecosystem following a period of succession. A climax ecosystem is one where the organisms immediately or eventually replace themselves in succession (depending on the temporal and spatial perspectives of the observer).

The concept of climax has proven too restricting for the new understanding of ecosystems as dynamic systems in a hierarchy of supersystems and subsystems. Succession remains a useful concept as long as it is understood to be a characteristic of all ecosystems and of all supersystems and subsystems if the observer chooses broad enough perspectives, and that it does not lead to an equilibrium condition (it does not cease) unless the observer chooses very narrow perspectives. At relatively
small spatial scales, succession is the process that drives the patch dynamic of ecosystems.

1.5.6.2 Patch Dynamics

The patch dynamic is the characteristic process of ecosystems whereby internal patches of disturbance routinely result in local succession, and the entire ecosystem remains in a heterogenous condition (Pickett and Thompson 1978, Pickett and White 1985). Patch dynamics are characteristic of all ecosystems at some scale. The disturbances may be natural, (e.g., tree death) or caused by humans (e.g., forest swiddens). Loucks (1970) pointed out that periodic disturbance at moderate to low levels maintains a maximum number of species in an ecosystem (the Intermediate Disturbance Hypothesis).

1.5.6.3 Niche

In 1944, Hutchinson provided the first modern definition for the ecological niche. It is the "sum of all the environmental factors operating on the organism; the niche thus defined is a region of an n-dimensional hyper-space, comparable to the phase-space of statistical mechanics."

Most modern ecologists have broadened this definition so that a niche now is understood to be the combination of all the environmental and behavioral variables that define and limit a population's interactions with the environment(s) and other

1.5.6.4 Ecotones and Edges

An ecotone is a transition zone between ecosystems where components are physically mixed, but where interactions among components are more probably intra-ecosystem than inter-ecosystem. Ecotones function as filters across which organisms and materials pass between ecosystems (Hansen, di Castri, and Naiman 1988; Hansen, di Castri, and Risser 1988; McCoy et al. 1986).

Edges are special cases of ecotones between relatively natural ecosystems and highly disturbed or non-native ecosystems (Harris 1988, Levenson 1981, Lovejoy et al. 1986, Ranney et al. 1981, Yahner 1988). Janzen (1986) observed that edges are not stationary and will often migrate toward the core because of extrinsic influences (e.g., fire propagation and seed rain from non-native or edge species). The edge effect is the zone extending into the ecosystem within which the ecosystem’s form and/or functions are changed by the existence of the edge.

Ranney et al. (1981), using indices of tree growth in old patches of temperate forest, found that basal area and stem density of trees and saplings were always lower than average in a band extending at least 15 m into the forests. Reporting in 1986, Temple measured edge effects for bird populations extending at least 100 m into the
interiors of temperate forest patches. Working with newly created patches of tropical rain forest, the Minimum Critical Ecosystems Project of Lovejoy et al. (1983, 1984, 1986) produced results including rapid changes in the microclimate at the new edges and rapid invasion by edge (including some non-native) species. Within 10 m from a man-made edge, bird species dropped 38% over birds 50 m into the forest and 60% over species counts 1 km into the forest. Edge species of butterflies penetrated 200-300 m into the forest. Other vectors of edge penetration include grazers, predators, and parasites (Harris 1988). Yahner’s (1988) review article reports that vegetation change typically extends 15 m into the forest patch, while population changes for sensitive and highly mobile species, especially birds, extend typically 100 m and as much as 600 m into forest patches. Temple and Cary (1988) and Wilcove et al. predicted typical edge effect penetrations of at least 200 m and as much as 600 m. Ranny (1981) and Lovejoy et al. (1986) reported that new edges in forest are quickly "scabbed over" by a cover of vines and weeds, followed eventually by light tolerant tree species. This may result in the initial shock of edge creation being followed by long-term buffering of micro-climate impacts.

1.5.6.5 Hierarchy

Clements’s (1936) organismic view of climax vegetation was opposed to the perspective of Gleason (1922) that vegetation was simply the chance result of species distributions along environmental gradients. Both perspectives are simplistic for ecosystems (even for vegetation-defined ecotopes). General Systems Theory deals
with far more complexity than either perspective can accommodate. In particular, a section of systems theory that deals with hierarchies has made very significant contributions. According to hierarchy theory, higher levels in a nested hierarchical system are the context for, constrain, spatially and temporally contain, and have less bond strength than lower levels. Higher levels are populated by larger entities, have slower reaction times and slower moving cycles, and have emergent properties not always predictable from examination of lower levels (O'Neill 1979; O'Neill et al. 1986, 1989; Urban et al. 1987). There are disturbance regimes at all hierarchical levels of ecosystems, and each level limits and is limited by its disturbance regime in different ways (Allen and Hoekstra 1987).

1.5.6.6 Synthesis

All ecosystem concepts presented here and recommended for retention have certain things in common. They are highly stochastic. Succession, patch dynamics, and ecotones are the resultant phenomena of stochastic processes. Niches are the Hamiltonian attractors for populations within ecosystems. All four concepts are believed to operate differently at different levels of ecosystem hierarchies. These concepts impart to the ecosystem a fuzzy and variable presence in both space and time, even when the ecosystem is defined at the level of the vegetated ecotope.
1.5.7 Ecological Equilibrium, Stability, and Steady-state

Early ecologists used the concept of equilibrium in conjunction with climax theory. As the climax concept lost support, so did the notion of ecosystem equilibrium. This is appropriate since formal equilibrium (a thermodynamic concept) cannot properly be applied to open systems (Ulanowicz 1986, pp. 9-27). Instead, most ecologists now prefer the concepts of steady-state and stability and related concepts of resilience, persistence, and resistance.

A steady-state system is one in which energy input and utilization is sufficient to maintain the system’s level of complexity (organization) (Ulanowicz 1986, pp. 9-27). For an ecosystem in steady-state, there exists a domain of attraction within which perturbation results in recovery to the original state. Species populations rise and fall, but persist. Outside the domain of attraction, the ecosystem follows a trajectory to a different state, becoming, in the process, a different kind of ecosystem. The trajectory may be predictable or chaotic (Holling 1973, 1986). Ecosystem simplification or collapse is the process of transition to a state with less, or much less, diversity. Some ecosystems must be thought of as multi-state in that they oscillate between different steady-state conditions (Holling 1986). Stability is the tendency of an ecosystem to remain in a steady-state condition. Metastability is the tendency to remain within a bounded region of multiple steady-state conditions (Holling 1973, 1986; Pimm 1986; Walker 1989).
Stability has corollary characteristics. Resilience can be thought of as the system's resistance to movement outside its domain(s) of attraction, or alternatively, as proportional to the size of the domain(s) (Holling 1973). Pimm (1986) prefers to define resilience as the measure of tendency to return to steady-state, and resistance as a measure of the strength of a perturbation required to move an ecosystem from steady-state. For Pimm (1986), persistence is proportional to the time an ecosystem can maintain its steady-state condition in the presence of a perturbation.

It is very likely that multi-state ecosystems that must periodically react to perturbations (e.g., coastal ecosystems subject to tropical cyclones) are more resilient and therefore very stable within more than one spatially and temporally large domain of attraction (metastable, hereafter conceptually included with stable) (Holling 1986; Trudgill 1977, pp. 111-145). Other factors positively correlated with stability are the redundance of trophic pathways (King and Pimm 1983; MacArthur 1957; Pimm 1984, 1986) and less trophic complexity (fewer trophic levels) (Gardner and Ashby 1970, Holling 1986, May 1972, Pimm 1986).

Measures of stability at one hierarchical level cannot be used to make inferences about stability at other levels (Botkin 1980, 1990; Holling 1986; Risser 1987; Risser et al. 1984). Stable systems may contain and may be contained by unstable systems.
1.5.8 Landscapes are Ecosystems of Ecosystems

1.5.8.1 The Concept of Landscape

Whittlesey (1954) defined the geographer's region as "an uninterrupted area possessing some kind of homogeneity at its core, but lacking clearly defined limits." Using essentially this definition, generations of geographers have defined "natural regions" and natural region methodologies (Bailey 1976; Dasmann 1972; Herbertson 1905, 1913; Klink 1974; Roxby 1926; Stamp 1957; Young et al. 1983).

The German geographer Richthofen (1883) first introduced the concept of the landscape (landschaften) as a unit of study comprised of a spatially related association of landforms (James and Martin 1981, p. 167). A landscape can be thought of as a natural region of associated landforms supporting a mosaic of interacting ecosystems (human systems and ecotopes) (Forman 1987, Klink 1974, Risser et al. 1984, Troll 1950, Zimmerman and Thom 1982, Zonneveld 1981). Forman and Godron (1986, pp. 9, 594) refined the definition, so that a landscape is a mosaic of biologically interacting, spatially inter-connected, and phylogenetically related ecotopes. Within the landscape, biological, geomorphic, and anthropomorphic processes are related.

The landscape is thus a natural (ecological and geographical) region within which ecosystems are more likely to interact with each other than with ecosystems outside the region. It is a locus of inter-ecosystem flows with very fuzzy edges. Its core of homogeneity is the probability cloud of potential interactions among ecotopes.
1.5.8.2 The Kinds of Ecosystem Interactions in a Landscape

In 1991, six agencies co-sponsored a workshop on ecosystem classification and conservation criteria for the South Pacific (see Appendix A). One of the products of that workshop was a list of some ways that ecosystems interact (Pearsall 1991b, 1991c). Many species require habitat components in more than one ecosystem, and nutrients and other materials are carried by the vectors of wind, water, and animals between ecotopes. In addition to these common interchanges, the workshop recognized several additional ecosystem functions that result in significant impacts in other ecosystems, and as a result, that have special value for conservation evaluation. These are:

a. storage of soil, nutrients, water, or contaminants, generally influencing adjacent or down-slope ecosystems;
b. reduction of landslips and surface erosion;
c. accumulation of soil and stabilization of land (e.g., mangroves);
d. fixing or buffering of nutrients and contaminants;
e. sheltering adjacent ecosystems from the impacts of winds and waves, salt spray, dust, and the lateral erosion of streams;
f. enhancement of water infiltration (ground water recharge), and storage of water as soil moisture, as ground water, or in surface wetlands;
g. soil enrichment;
h. capturing occult atmospheric moisture, adding water to the water budget of the watershed; and
1. provision of temporary habitat for young (reproduction and nursery habitat), migrants, or refugees.

1.5.8.3 Landscape Size and Hierarchy

The concept of landscape is not adimensional. Jackson (a landscape geographer) defined the landscape as a unit of land existing at a scale most suitable for study using remote sensing (reported and endorsed in Forman and Godron 1986, p. 7; also see Risser et al. 1984). Aerial photos represent a range of approximate coverages from 1 km² to 250 km². SPOT satellite scenes cover approximately 3,600 km² (Chevrel et al. 1981). Landsat Multi-Spectral Scanner and Thematic Mapper scenes cover approximately 32,000 km² (Chaudhury 1985). Given this range of dimensions (roughly 1-30,000 km²) and rejecting the end points as extreme, landscapes usually occur with sizes ranging from tens to thousands of square kilometers.

Mindful of hierarchy theory and desiring to place the landscape in a hierarchy of ecosystems, Bailey (1987) proposed that the regional (larger) ecosystem be determined mainly by the eco-climatic zone (sensu Köppen 1931), that landscapes be determined mainly by associations of related landforms (sensu Hammond 1954), and that the smaller ecosystem (the ecotope) be determined by the vegetation association. The order of sizes suggested by the limitations of remotely-sensed data discussed above coincides very well with Bailey’s recommendation.
1.5.8.4 Landscape Stability

An ecologically stable (or metastable) landscape can be defined as one where the patterns and processes of component ecotope interaction are changing relatively slowly and where entropy gradients are shallow. In an ecologically stable landscape, component ecotopes will persist without simplification or collapse, and the ordinary processes of material and biological interaction among them will not change rapidly (Baker 1989, DeAngelis and Waterhouse 1987, Gardner and Ashby 1970, Hill 1987, Holling 1973, May 1978, Pimm 1986).

1.5.9 Landscape Ecology

von Humboldt was possibly the first landscape ecologist. He based his keen analyses of climatology and vegetation ecology on critical observation and subtle description of the landscape, der totale character einer Erdgegend (the total character of a patch of the earth) (Neef 1982, Zonneveld 1990). Richthofen (1883) suggested that the landscape should be a fundamental unit of geographical studies. Following Richthofen's lead, Passarge (1923) attempted to formalize the study of landscapes. He defined the landscape in terms of a mosaic of vegetation types and mapped the landscape zones of the earth (James and Martin 1981, pp. 181-182). Sauer (1925) provided a simplified overview of Passarge's system for American audiences. Although Sauer's interpretation was briefly popular in North America, Passarge's complete system of ecological landscape description and classification did not find lasting favor because it was too complex, it incorporated complex and unfamiliar
Troll (1939, 1950) first defined the discipline of landscape ecology as the study of the physical and biological relationships that operate among the spatial units of the landscape. The landscape was defined then as the unit of land within which a suite of ecotopes consistently exist and interact. Troll explicitly stated that at the scale where ecotopes interact, remotely sensed data is required for study and analyses, and landscape ecology has long been closely tied to the interpretation of aerial photographs and, more recently, satellite data (Dale et al. 1989, Klink 1974, Neef 1982, Risser 1987, Risser et al. 1984, Troll 1971).

Troll and early students of landscape ecology were German geographers. Unfortunately, they initially had little dialogue with geographers outside of Germany because "landschaften" translates in other languages to words with little explicit spatial meaning (e.g., "landscape" in English, with its several meanings, remains a persistent problem) (Klink 1974, Neef 1982). Early landscape ecology programs and initiatives in Europe were those of the International Institute for Aerial Survey and Earth Science (The Netherlands), the Institute for Landscape Care and Protection at the Technical University of Hannover (Germany), the Central Institute of Vegetation Mapping (Germany), the Institute of Theoretical and Applied Phytosociology (Germany), and the Geographic Institute at the University of Münster (Germany).
(Naveh and Lieberman 1990) (Schreiber 1990). The titles of these institutions indicate the breadth of the emergent discipline.

Beginning in the 1960s, Christian at the Commonwealth Scientific and Industrial Research Organization of Australia (Christian 1959, Christian and Steward 1968), Rowe at the University of Saskatchewan (Rowe 1961, Rowe and Sheard 1981), and Hills with the Ontario Department of Lands and Forest Resources (Hills 1961) all made early applications of the landscape-wide, hierarchical, systems approaches developed by European landscape ecologists. Their applications were mainly large regional ecosystem surveys in which substrate and vegetation association (ecotope) were the basic mapping units (Risser et al. 1984, Rowe 1988).

The first major impact of the discipline of landscape ecology on American scientists apparently occurred when four ecologists and a geographer (Carlson, Fabos, Forman, Golley, and Sharpe) attended the 1981 meeting of the 600 member Netherlands Society of Landscape Ecology. Based on that experience, a National Science Foundation grant was raised to support a Workshop on Landscape Ecology in the United States (Forman 1990a). In 1983, a group of 25 scientists assembled at Allerton Park, Piatt County, Illinois to "outline the disciplinary area of landscape ecology, to evaluate the potential of such a discipline, and to describe its application to basic and applied natural-resource issues" (Forman 1990a, Risser 1987, Risser et al. 1984). It is interesting to note that the emphasis at that first meeting was on
applications of landscape ecology, often to conservation issues. It is also interesting to note that only one of the 25 scientists was a geographer, the rest being ecologists and a few foresters. An 18 page monograph was published (Risser et al. 1984) describing landscape ecology as the ecology of heterogenous environments.

Landscape ecology can be considered a sub-discipline of either geography or ecology. It probably should be considered a transdisciplinary science with roots in both fields. It is sad that the American geographic community has essentially abdicated the field. In an attempt to distinguish geography from ecology, Fosberg (1976, p. 118) once defined geography as the

"discernment and delineation of landscape patterns, interpreting the structures and processes that give rise to them, and developing an understanding of their significance in biological and human terms."

Given the formal definition of landscape and recognizing structures and processes as ecosystemic features, Fosberg's definition fits landscape ecology very well.

Contemporary attempts to refine the definition of landscape ecology tend to fall into two schools which show signs of joining a debate. One is more inclusive, declaring landscape ecology to be a holistic science. It should deal with all aspects of the structural and functional appraisal, history, planning, management, conservation,
and restoration of landscapes, treating these as systems, and accounting for their emergent properties (Naveh 1982, 1991; Naveh and Lieberman 1990; Zonneveld 1990). The other is more exclusive, attempting to shift landscape ecology to a post-structural science. Having spent the last 50 years studying the shape, distribution, and orientation of landscape structural units (patches, corridors, networks, etc.), e.g., Forman and Godron (1986), landscape ecology should now be in transition to the study of the role these structural units and their spatial vectors play in the ecosystemic functioning of the landscape (Merriam 1988, Neef 1982, Zonneveld 1988). The difference is small, and both schools emphasize applications.

1.5.10 The Theory of Landscape Ecology

The theory of landscape ecology has not been succinctly stated and identified as such, although it is acknowledged in all of the works in the discipline (Antrop 1988; Birkeland and Groenenbaum 1985; Baudry 1984; Baudry and Merriam 1988; Forman 1982, 1990; Forman and Godron 1984, Jansson et al. 1988; Merriam 1984, 1988; Rastetter 1991; Risser 1990; Swanson et al. 1988; Turner 1989a). The theory can now be stated: The biological and material interactions among ecosystems are highly (often mainly) influenced by their relationships in geographical space.

The principle that conservation should be integrative and organized at the scale of the landscape was developed in previous sections by ascending the hierarchical ladder from species to ecotopes to landscapes while seeking an adequate basis for
conservation. This principle is actually the conservation corollary of the theory of landscape ecology and can be restated: The process of measuring, modelling, and preserving the spatial relationships among ecosystems provides a useful, approximating approach to understanding and conserving the interactions among the ecosystems (ecotopes) of landscapes, and thus, the stability of the landscapes themselves.

1.6 Islands are Special Landscapes

Islands comprise the membership of a very special class of landscapes. In this thesis, the focus is on oceanic islands, which are defined here as islands surrounded by oceanic waters and populated exclusively by species or the evolutionary descendants of species that dispersed to the islands across oceanic waters. This distinguishes oceanic islands from continental islands, that are the never-submerged but now detached pieces of continental plates, and from islands in lakes and streams. These islands share many of the biological and ecological (but not geological) features of oceanic islands, but these features are less pronounced and less influential.

1.6.1 Island Ecology

The substrate of oceanic islands is usually either volcanic or sedimentary. If the former, it is most often basaltic. If the latter, it is most often coral and the erosional products of coral (Thomas 1963).
The ecosystems of oceanic islands have a number of distinguishing characteristics. Several texts exist on the subject of island ecology (Carlquist 1974, Fosberg 1963a, Gorman 1979, Mueller-Dombois et al. 1981, and Williamson 1981). In general, these authors and others find that island ecosystems are most strongly influenced by isolation, small size, youth, and periodic disturbance (Dahl 1984, Fosberg 1963b, Mueller-Dombois 1981). As a result, certain ecological characteristics are prominent.

Island ecosystems generally have fewer species than similar-sized, ecologically comparable mainland systems. On young, volcanic islands, this is the result of youth, and the difficulty of dispersal to islands. On coral islands, it is the result of reduced habitat diversity. Carlquist (1974) calls these phenomena "disharmony."

Island species are likely to evolve more rapidly than their mainland congeners, especially through adaptive radiation resulting in the derivation of many closely related species from a common ancestor. Straight-line evolution is likely to result in phenotypic polymorphism. These effects are believed to be the result of lower competition and the availability of more habitats resulting from fewer species (Diamond 1984, Mueller-Dombois 1981). An interesting side-effect of this trend is that species with high dispersal ability are likely to arrive on islands and evolve into new species to fill niches occupied by poor dispersers on the mainlands, losing their own dispersal abilities in the process. Thus, on islands, one can find flightless birds.
occupying niches that, on mainlands, would be occupied by rodents, reptiles, and small mammals (see especially Carlquist 1974, chapters 3-9).

Island species are also more likely to become extinct than their mainland congeners. Apparently the main reasons for this are the lack of heterosis in small populations and the influence of dramatic environmental fluctuations (e.g., droughts, cyclones, volcanos) (Dahl 1984, Mueller-Dombois 1981). The cycle of colonization, evolution, and extinction common to islands has been termed the "taxon cycle" by Wilson (1963) and others (Ricklefs and Cox 1972).

Islands tend to be receptive to invasion by new species. Before humans began assisting species with their dispersal, new species arrived and became extinct or successfully joined island ecosystems relatively slowly. With human assistance, species invasions are extremely rapid. For example, in 1778, the islands of Hawai‘i supported 950 flowering plants of which 862 were endemic. Some of the remainder were imported by the original Polynesian colonists. By 1986, there were approximately 6,000 species of flowering plants in Hawai‘i, and more than 30 of the original 950 were extinct. Of the 6,000 species, 856 were considered to be naturalized (weeds) (Dr. Cliff Smith, personal communication). The ecological

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4Hereafter, "native" species refers to those that arrive on islands without the assistance from humans or their domestic animals or machines. "Non-native" species are those that invade with direct or indirect human assistance.
consequences of rapid invasion by non-native species and accelerated extinction of native species are poorly understood.

A few generalizations are available about the process of invasion. Invading predators tend to be much more successful than invading competitors. Many island species evolved in the absence of predators. There is, on the other hand, little evidence that island species are competitively disadvantaged (Mueller-Dombois and Howarth 1981). However, failure of species to successfully invade appears to be positively correlated with their morphological similarity to their most closely-related native congeners (Moulton and Pimm 1986, also see Hutchinson 1959). Successful invasion is more likely in the presence of environmental disturbance, especially if the disturbance is caused by non-native species (e.g., pigs, humans) (Mueller-Dombois 1981, Mueller-Dombois and Howarth 1981). Finally, scientists disagree about whether the success of invasion is correlated with the number of species already present (Moulton and Pimm 1986, Mueller-Dombois and Howarth 1981).

Because of periodic disturbance, island ecosystems can rarely be considered stable. Most island ecosystems exist naturally in very large domains of metastability within which steady-state conditions (constant patch dynamic mosaics) are very rare or non-existent (Shugart and West 1981). Island species and ecosystems are ephemeral.
Tropical cyclone Ofa in Western Samoa provided a few insights into the differential impacts of a major environmental disturbance on ecotope resilience as influenced by human disturbance and the presence of non-native species (Pearsall and Whistler 1991b). During and after the cyclone:

a. native forests fared much better than non-native forests;
b. undisturbed native forests fared better than disturbed native forests;
c. larger occurrences of native ecotopes fared much better than smaller occurrences of native ecotopes; and
d. contiguous native ecotopes fared better than isolated native ecotopes.

1.6.2 Island Biogeography

The Equilibrium Theory of Island Biogeography has its roots in the analyses of species/area relationships that have long been a popular component of population ecology (Arrhenius 1921, Connor and McCoy 1979, Gleason 1922, Preston 1962, Wright 1988). The theory, first proposed by MacArthur and Wilson in 1963 and refined in 1967, states that the number of species on an island will vary directly with its area and inversely with its degree of isolation as immigrations and local extinctions reach an equilibrium point.

A habitat island is an isolated area of habitat, and is defined with reference to a particular species or group of species. When a habitat island is disconnected from a larger area of habitat, it will initially have more species than it can support, so its
species number will decline (relax) for a while. A newly emerged volcanic island will have fewer species than it can support, so, for a while, it will gain species by immigration until an equilibrium point is reached.

Although the theory seems intuitively true, it is not popular. Some of its detractors provide evidence that habitat diversity is far more important than area as a basis for species richness (Gilbert 1980, Karr 1982). This criticism stems from a basic misapprehension of the intent of MacArthur and Wilson who stated that area was a partial surrogate variable for habitat diversity.

Other authors consider only some species (e.g., birds) and attempt to extend their conclusions to the number of all species, a dangerous extension given that, on islands, birds tend to represent a disproportionate number of species because they migrate easily and radiate rapidly resulting in high species diversity (Diamond 1984). The best experimental test of the theory was conducted by Simberloff on experimentally defaunated mangrove islands in Florida (Simberloff 1969, 1970; Simberloff and Wilson 1969). This study provided mild support for the theory, but, given the pioneering nature of the mangrove ecotope, it is unlikely that dispersal was significantly limiting in the experiment.

It is debatable whether the theory can be applied to habitat islands on continents or to subdivisions of actual islands (Levinson 1981, Loman and Von...
Schantz 1991). Whitcomb (1977) reported some support for the theory as applied to habitat islands. Brown pointed out that non-equilibrium situations are more common in patches of habitat, especially as is usually the case, when dispersal is not limiting (Brown 1971; Brown and Gibson 1983, pp. 460-491). In the best study yet done on habitat islands, Lovejoy et al. (1984, 1986) reported that following the creation of new habitat islands in the Amazon, the isolates are temporarily invaded by birds seeking refuge, and in fact, the number of species goes up temporarily, although for all groups monitored (e.g., birds, primates, butterflies), some original species are lost over time.

The term "equilibrium" was not intended to extend to evolutionary time scales, but to be restricted to generational time scales. That is, the equilibrium point was expected to move toward greater numbers of species in evolutionary time. Application of the theory to oceanic islands is confounded by high rates of evolution and low rates of invasion, blurring the distinction between evolutionary and generational scales. Frequent natural disturbances on these islands result in periodic, stochastic extinctions (e.g., Abbott and Grant 1976) so that equilibrrial conditions are rare.

The theory was originally based on the observation that larger and less isolated oceanic islands tend to support more species than smaller oceanic islands, all other variables being held constant. Whether this is equally true for habitat islands is
problematic. It is doubtful that the theory explains any phenomena more complex than the observations on which it was founded.

1.7 Ecologically Stable Landscapes and Islands: Summary

Biological diversity can be described as the information content of an ecosystem. There are many reasons for conserving biological diversity, not least of which are conserving ecosystem functions and the evolutionary capacities of species. Both species and ecosystems must be conserved. When attempting conservation at larger scales, ecotope conservation is a good first step or coarse filter strategy.

The niche is the combination of all the environmental and behavioral variables that define and limit a population’s interactions with its environment. The ecosystem can be described as the set of populations and the subset of their niches within which internal interactions are more likely than external interactions. Ecosystems generally have very fuzzy edges, because they are probabilistic loci of component organisms, substrates, and their interactions.

Ecosystems are probably never in equilibrium, but they may be stable or metastable, exhibiting varying degrees of resistance, persistence, and resilience. A stable (steady-state) ecosystem oscillates around an attractor within a domain of attraction. Metastable ecosystems oscillate around more than one attractor in the (usually much larger) domain.
Ecosystems are hierarchically nested systems. Ecosystems at the scale of the vegetation stand and landform are classed as ecotopes. Ecosystems at the level below ecotope constitute the patches of the patch dynamic, and it is the oscillation of these patches around a domain of attraction that maintains diversity in the ecotope. The ecosystem of ecotopes is the landscape, with size ranging from tens to thousands of km². Landscape ecology is the study of interactions among ecotopes in the landscape.

Oceanic islands are a special case of landscapes. Giving first priority to conservation of ecosystems on islands is an attractive option because the species composition of island communities is in constant flux, and extinctions are natural and common. The taxon cycles of islands tend to be quite rapid. On the other hand, oceanic islands are especially problematic as landscapes for conservation because their ecosystems typically are metastable, and naturally oscillate within very large domains of attraction. That is, they undergo periodic and often severe perturbations and cannot reasonably be considered to exist in a steady-state condition at any time. Oceanic island ecosystems are probably very resilient within the confines of their large, natural domains of attraction.

The invasion of island ecosystems by new species and the extinction of existing island species have been accelerated by humans, sometimes by orders of magnitude. Non-native species that physically disturb the environment or that prey on native species have more severe impacts than non-native species that merely compete
with native species. The long range ecological consequences of these changes are not known. Evidence from Western Samoa indicates that the impacts of perturbations are exacerbated by the accelerated influx of species.

1.8 Operational Questions

Can the systematic application of principles from landscape ecology and other branches of geography and, to a lesser extent, conservation biology be used to develop a geographic model adequate for the planning and development of nature reserve networks at the scale of whole landscapes? Will such networks function to conserve the ecological viability of the landscapes including their human populations?

The research problem can now be restated:

Can the definition and analysis of ecotopes by inventory, cartographic modelling, and the use of spatial statistics provide an effective method for determining conservation priorities. Can conservation networks be designed based on those priorities in order to conserve effectively the ecological stability of landscapes?
CHAPTER 2

ECOLOGICALLY STABLE LANDSCAPES:
BACKGROUND ON METHODS AND TOOLS

2.1 Introduction

This chapter provides an overview of four groups of methods and tools useful for translating conservation science into conservation action. These include ecosystem classification, tools for landscape inventory and analysis (including cartographic models and geographic information systems), approaches to the selection and design of nature reserves, and approaches to designing networks of nature reserves. The review is tailored to the research covered by this thesis, and more attention is given to newer, more controversial, and/or more critical topics, with less attention going to well established methodologies, especially when they are not central to the theme of this research.

2.2 Classifying Ecosystems

Various attempts have been made to develop universal systems of vegetation classification (e.g., IUCN 1973, UNESCO 1973; history and discussion in Fosberg and Pearsall in press). Most of these suffer from certain conceptual problems. Most do not provide for secondary or disturbed vegetation; most are operational only at a single spatial scale (e.g., that of the stand, association, or formation); most require a particular temporal perspective (e.g., the past for presettlement vegetation, the future for potential

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1Much of this section was modified from Fosberg and Pearsall (in press) and Pearsall (1991c).
natural vegetation), and most (except Fosberg 1967) do not adequately separate the vegetation from the physical environment. They usually are, in fact, poorly formulated ecosystem classifications. Classification schemes for animal habitats and for non-vegetated ecosystems (e.g., those of caves) have generally suffered from similar problems (Fosberg and Pearsall in press). A solution to this confusion is to classify ecosystems deliberately rather than vegetation or habitats, and to do so in a way that is useful at different scales. An ecosystem classification that was functionally and spatially hierarchical would be tremendously useful to the effort to conserve ecosystems.

Rules for an ecosystem classification can be extracted from hierarchy and general systems theories and from the general discussion of ecosystems in the previous chapter (especially Feibleman 1954; Grigg 1967; O'Neill 1979; O'Neill et al. 1979, 1986, 1989; Rowe 1961; Schultz 1967). The classification must be understood to contain both types and entities. An ecosystem type is analogous to a species (e.g., Canis familiaris is the taxonomic type for the domestic dog). The individual occurrences of ecosystems (e.g., ecotopes) are entities and are analogous to individuals of a species (e.g., Rex is an individual dog). The individual occurrences of ecosystems are classified according to their conformance to the type criteria (we know Rex is a dog because he conforms to the definition of Canis familiaris). Classifying variables for types and entities are the same (the same rules that distinguish all dogs from all cats are the rules that make us certain that Rex is a dog and not a cat).
2.2.1 Type Rules

a. All ecosystem types at intermediate levels are included taxonomically in
types at the next higher level, and collectively they include all the types
at the next lower level. There are usually more types of ecosystems at
each lower level;

b. No ecosystem type at any level can be included in more than one type at
the next level up;

c. At any given level, all the ecosystem types are mutually exclusive and
(potentially) collectively comprehensive;

d. Every ecosystem type has diagnostic characteristics, and types at higher
levels are easier to distinguish than types at lower levels (fish are easier
to distinguish from mammals than the various species of fish are to
distinguish from each other);

e. As knowledge improves, ecosystem types may be combined or split
without changing levels; and

f. Types at one level can be reclassified from one type to another at the next
higher level (e.g., genera can be reclassified from one family to another).

2.2.2 Entity Rules

a. Ecosystems (entities) at one level will be spatially larger and will contain
more elements (e.g., species, substrate elements) than ecosystems at the
next level down;
b. The reaction times of ecosystems at higher levels are longer than the reaction times of ecosystems at lower levels;

c. Ecosystems at higher levels may exhibit emergent qualities, but their behavior is largely determined by the aggregate behaviors of their member entities (species, sub-ecosystems, etc.); and

d. Ecosystems at higher levels constrain and control ecosystems at lower levels through feedback mechanisms.

2.2.3 Synthesis

The highest level of ecosystem classification is the biosphere, where the one class and the one entity are identical (pending the discovery or manufacture of other biospheres). Landscapes form a level below the biosphere. Between these two levels fall the various biogeographic and eco-geographic natural regions defined by various ecologists and geographers. The workshop on ecosystem classification and conservation in the South Pacific (Pearsall 1991c) felt that below the landscape level, terrestrial ecosystems should be classified\(^2\) as:

a. Formations -- defined by vegetation physiognomic unit, topographic position, and moisture regime;

b. Sub-formations -- defined by leaf structure and seasonality and community stratification;

\(^2\)Note that the first two tiers are defined by structure and the second two tiers are defined by composition.
c. Associations -- defined by characteristic substrates and genera of plants and animals; and

d. Ecological Units -- defined by characteristic species.

This present research required the development of an ecotope classification for Western Samoa. Vegetation was defined at the level of the formation, and then landtypes (landform associations) were substituted for the substrate information. The unique combinations of vegetation and substrate were considered to be ecotopes (sensu Tansley 1939).

2.3 Tools for Landscape Inventory and Analysis

2.3.1 Remote Sensing of Ecotopes

The use of remotely sensed data for ecological analysis is virtually diagnostic of landscape ecology. The various ranges of scale were presented for aerial photographs and SPOT and Landsat satellite images. The resolution of aerial photographs varies with the focal length of the camera, the clarity of the lens, and the grain size in both the negative and the print. The resolution of Landsat Multi-spectral Scanner and Thematic Mapper images is 79 and 30 m respectively. The resolution of SPOT satellite images is 10 m for the panchromatic sensor and 20 m for the radiometric sensors (Campbell 1987, pp. 149-153; Chaudhury 1985; Chevrel et al. 1981). The analysis of aerial photography is thoroughly discussed in many elementary and intermediate texts (e.g.,
Campbell 1987, Lillesand and Kiefer 1979) and is not further elaborated here. The applications of satellite data are less generally understood.

Landsat and SPOT satellite images are useful for ecotope inventory and analyses because the reflectance of the earth's surface is selectively sampled within certain bands (ranges of wave length). Table 2 provides this information for the SPOT satellite.

<table>
<thead>
<tr>
<th>BAND</th>
<th>COMPUTER COLOR</th>
<th>WAVE LENGTH</th>
</tr>
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<tbody>
<tr>
<td>Panchromatic</td>
<td>Black and white</td>
<td>.51-.73 μ</td>
</tr>
<tr>
<td>Yellow-green</td>
<td>Blue</td>
<td>.50-.59 μ</td>
</tr>
<tr>
<td>Red</td>
<td>Green</td>
<td>.61-.68 μ</td>
</tr>
<tr>
<td>Near Infrared</td>
<td>Red</td>
<td>.79-.89 μ</td>
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</table>

Jensen (1983) provides a list of nine fundamental ecological variables that can be measured or estimated from satellite data. These are planimetric location, topographic-bathymetric elevation, color and the spectral signature of features, chlorophyll absorption, vegetation biomass, vegetation moisture content, soil moisture content, surface temperature, and texture. In each case, the ability to extract useful data from the satellite data depends on the ability to interpret the relative reflectance values of the various bands.
In order to determine planimetric location, contrast enhancement is often a necessary intermediate step in the use of satellite data. The purpose of contrast enhancement in satellite image processing is to improve one’s ability to distinguish between adjacent reflectance classes, that is, to define edges between groups of radiometrically similar pixels. The following discussion is based on Campbell (1987, pp. 280-283), Jensen (1986, pp. 117-178), and Lillesand and Kiefer (1979, pp. 562-573).

The histogram (pixel distribution) of reflectance values for a given band in a given image will typically be confined to one or few discontinuous ranges. Color saturation assignments (0-255) for the color computer monitor are uniformly distributed across the potential range of reflectance values. The resulting image shows very little contrast. The process of contrast enhancement consists of setting lower and upper thresholds of reflectance for evaluation while excluding regions of the image that are not relevant to the evaluation or where reflectance values are very low. When a mask is used in advance of this process, setting the threshold limits is much easier. Color saturation assignments are set to zero below the lower threshold and to 255 above the upper threshold (assuming a typical color range of 256 values, from 0-255). This leaves 254 color saturation assignments available to distribute between the thresholds. Dramatic contrast enhancement is the result.
The three questions that must be answered in the process of contrast enhancement are:

a. whether to operate on the original reflectance values of the various bands of satellite data or to create synthetic or compound variables based on the original data;

b. where to bracket the range for contrast enhancement; and

c. how to distribute color saturation assignments within the bracketed range. Options here typically include linear, natural and base-10 logarithmic distributions that may be distributed or clustered. Clustered distributions may be equi-populated or canonical (based on internal correlations).

The tessellation of a region into classes may be accomplished by contrast enhancement and manual edge definition, or it may be accomplished by using the computer to classify individual pixels. The classification may be supervised, in which case the classes are pre-defined and the final classification must conform to a training sample, or the classification may be unsupervised, in which case, the classes are not predefined, the computer is used to cluster pixel reflectance signatures into classes, and these are then defined from other planimetric sources or in the field. Estes, Franklin, and Steadman (1989) and Franklin and Steadman (1991) provide accounts of a habitat mapping project in the Cook Islands using aerial photographs and computer classified SPOT satellite imagery. Cloud cover over the islands was a severe
problem, and geometrically registering the satellite data to the maps in use was thus
confounded. The research team attempted both supervised and unsupervised
classifications of the data. In the latter case, a clustering algorithm was used to
extract 40 classes. Unfortunately, some of these contained more than one land-cover
type, and others ultimately had to be lumped into cover types. In both cases, with
much manual lumping and splitting, the team ultimately was able to produce useful
vegetation classifications.

2.3.2 Cartographic Views of Landscapes

Historically, the ecology of regional landscapes has been inventoried and
mapped from two general points of view. The first is the project specific perspective,
in which potentially limiting environmental factors are mapped and then overlaid to
evaluate their composite limitations. With a use in mind, the planner attempts to find
a place for it. This approach developed in many places, especially at Harvard (e.g.,
Steinitz et al. 1976) and the University of Pennsylvania (e.g., McHarg 1969). This is
still the more popular perspective (Tomlin and Johnston 1988), and it is the standard
approach of environmental consulting firms.

The second point of view is not project specific, but is driven by an interest in
whole landscapes or regions, and an interest in testing prior hypotheses about the
relative significance of specific environmental components in the composition and
functioning of ecosystems. This is the European tradition of landscape ecology, with

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its major emphasis on vegetation (e.g., Canters et al. 1991; Zonneveld 1988a, 1989). The most significant variant is the Australian approach to mapping and analysis of land systems with its major emphases on landforms and soils (e.g., Christian 1959, Christian and Stewart 1968). These two perspectives are summarized in Domon et al. 1989 as the "selective-qualitative" and "holistic-descriptive" approaches. In the United States, the former is still very popular, but the latter is gaining in popularity (e.g., Hendrix et al. 1988) based on impetus from systems ecologists (e.g., Odum 1969).

2.3.3 Cartographic Models of Landscapes

A model is a device for the prediction of the behavior of a complicated, poorly understood system based on the behavior of parts that can be understood. It is a structural formulation of our knowledge about a system. The more accurately a model represents reality, the more complex, difficult, and expensive it will be to use, so every model is a compromise between real complexity and manageable, useful simplicity (Peuquet 1988, 1991).

Chorley and Kennedy (1971, p. 7) discuss black box, white box, and gray box systems. A black box system is one where only inputs and outputs are specified. A white box system is one where all the internal processes of transition from input to output are specified. A gray box system is in between, with only some of its internal processes specified. A black box system can be thought of as a rule (given x, then
A white box system is a subset of reality. A gray box system is a model. Modelling is the creation of a relatively simple system to imitate a more complex system in order to gain some understanding of the latter (Hall and Day 1977; Kitching 1983; Trudgill 1977, pp. 1-15).

A model must be based on hypotheses of relevance, functions, and relations among the elements of a real system (Jeffers 1978, p. 163). A model is itself a hypothesis, and the single most useful product of a model is a new hypothesis that explains or predicts the behavior of the real system itself (Hall and Day 1977).

One basic approach to modelling is analytical, based on the quantification of functions and the simultaneous solution of difference equations. This approach is very difficult or impossible if the equations are non-linear, in which case functional behavior may be chaotic. Another approach is through simulation, or the successive iteration of multiple difference equations. This approach works even if the equations cannot be simultaneously solved, but the question of how processes function is rarely resolved (Caswell 1976, Hall and Day 1977). A third approach is structural, in which a model of the structure of a system is studied and measured in an attempt to understand processes. This approach provides useful insights into processes, but may be less useful for predicting results. Analytic and simulation models are highly deterministic. Structural models can model stochasticity (a dart board is a simple...
structural model of a stochastic process). A structural model of a subset of the surface of the earth is a cartographic model.³

The elements of a cartographic model include objects and fields (Goodchild 1989). The objects can include points, lines (segments, arcs, trees, networks), and polygons⁴ (isolated, adjacent, and nested) (Peuquet 1991). The model may not represent the surface of the region with polygons, or it may do so imperfectly or perfectly. In the last case, the surface is tesselated by the model. Cartographic models are spatially isomorphic models of geographic/ecological systems in which there is a one-to-one correspondence between system objects at some scale and model objects, and the spatial relationships among the former are more-or-less accurately represented in the latter (Hall and Fagen 1956). Fields, the regions of the variable influences that objects exert upon each other, may be represented in cartographic models by cartographic symbols such as arrows, by cartographic devices such as color intensity or hue, or by assigning numerical value to cartographic objects. In each case, a set of rules for object interaction based on the cartographic content must be specified.

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³All maps are cartographic models, but not all cartographic models are maps (e.g., structural profiles or transects).
⁴A cartographic polygon is simply a bounded area of a map. It is not synonymous with a mathematical polygon in which the boundary is composed of line segments of equal length.
Cartographic analysis includes the measurement of cartographic sizes, distances, directions, and weights; variation of cartographic scale and resolution; classification and reclassification of objects; measuring connectivity; statistical analyses of various neighborhood characteristics; statistical analyses of correlation between data types (e.g., Margules and Nichols 1987); and overlaying or combining data using algebraic or logical operations. These various operations are well covered by Berry (1987a, 1987b), Bracken and Webster 1990, and Tomlin (1990). Tomlin, in particular, provides a cogent text on the process of overlaying data, a process he defines as "map algebra." Brooker (1991), Haining (1989), and Trangmar et al. (1985) cover the process of extrapolating or generalizing point or line data to areal data (geostatistics).

Cartographic models of landscapes are particularly useful as structural models of the pathways of interactions among ecotopes. However, all cartographic tools can be misused. Two cartographic tools have special potential for producing error if used injudiciously. These are the ability to overlay multiple data sets and the ability to freely change scales.

2.3.4 **Error in Cartographic Models**

Before the specific problems of error in cartographic models of landscapes can be discussed, the more general problems of errors in geographic data must be introduced. Aronoff (1989) distinguishes between error sources that are specific to
individual objects (positional accuracy, attribute accuracy, etc.) and those that are specific to whole data sets (resolution, topological failures, data lineage, etc.). In contrast, Maffini et al. (1989) classify error as that which is attributable to the inherent properties of nature (e.g., fuzzy ecotones), that which is attributable to failures of measurement (accuracy, resolution), and that which is attributable to flawed analysis (flawed models, misapplication of models) (also see Burrough 1984, pp. 103-135; Goodchild 1989). In general, the processes of error generation and control in the measurement and placement of simple objects (points and line segments) is reasonably well understood, but very little is understood about error generation and control for more complex objects, and even less for fields (Goodchild 1989).

The problem of estimating error in cartographic models is confounded by the fact that estimations of error usually rely on having a more accurate model against which to compare the results (Aronoff 1989, Chrisman 1987, Lillesand and Kiefer 1979). Normally, the mere fact of preparing a cartographic model means there is not a more accurate model available for comparison (else use it instead!). Reality is, of course, exactly accurate, and the best tests of cartographic models are those that for a statistically adequate subset of nature make more reliable measurements than were used in the model's development. Unfortunately, real nature is rarely precise. For example, Maffini et al. (1989) point out that uncertainty about regional membership decreases with distance from a common boundary at a rate corresponding to the Gaussian (normal) distribution. The line itself can only be thought of as the most
probable location of the boundary, banded by concentric, amorphous regions of lower confidence. Estimating the distribution of uncertainty is highly dependent on independent measures of boundary placement, but the boundaries between most regions (e.g., between ecotopes) are very fuzzy in nature.

2.3.4.1 Overlaying Imperfect Data

The most widely recognized source of error in the use of cartographic models is through accumulation during the process of overlaying imperfect data (Bailey 1988, MacDougall 1975). Because ecosystems typically have fuzzy ecotones, ecosystem boundary data are imperfect by their very nature. Using the example of grid-based data, Veregin (1989) calculates that when error in the individual layers is spatially independent, then the proportion of correctly identified map cells varies directly with the product of the proportions of correctly identified cells for the individual layers. Accumulated error is not, however, as many assume, equal to the product of the errors.

Walsh et al. (1987), in overlay trials based on Landsat data, found that composite error ranged upward only as high as the error of the least accurate layer. Newcomer and Szajgin (1984) calculated that the probability of accuracy on gridded overlays was only slightly less than the probability of accuracy on the least accurate layer. Chrisman (1987) hypothesized that the limitation on error in overlay operations is an artifact of error in data sets from the same region being non-spatially
independent. For example, when soils and vegetation data are overlaid, many tiny polygons (slivers) will be created where boundary lines do not exactly meet. The presence of slivers is an indication of the non-spatially independent nature of error in soil and vegetation data. Slivers are generally treated by simply eliminating polygons below some tolerance level of area (e.g., that comprise less than 0.5% of the surface). When multiple layers of non-independent data are overlaid, slivers tend to cancel, and the final boundary's location is near the center of its probabilistic range.

2.3.4.2 Changing Scale

When using cartographic models of ecosystems or any other class of objects existing in a hierarchy, it is dangerous to change scales between data collection, analysis, and modelling. Hierarchical layers have emergent properties, and the relationships between layers sometimes operate in unpredicted ways. Variations in scale result in very different processes coming into focus, and generalizations across scales are dangerous (Risser 1987, Risser et al. 1984). Generalizing downward from higher, larger scale observations is known as the ecological fallacy, while generalizing upward from local observations is known as spatial transmutation (King et al. 1991, Meentemeyer 1989, Meentemeyer and Box 1987, O’Neill 1979). The latter is not inherently fallacious, but it does require caution, and a statistically adequate sample.

Scale changes select differently among data types. In a series of trials using maps of eastern Tennessee, Turner et al. (1989) found that as scale and resolution
decreased, land cover types that were clumped disappeared much more slowly than types that were dispersed. Type diversity decreased linearly with resolution while dominance and contagion (adjacency) increased as resolution decreased as long as the number of cover types remained constant. Dominance and contagion then declined sharply when a type dropped out. This resulted in a slow-climb, sharp-drop, zigzag curve for both variables.

2.3.5 Geographic Information Systems

Geographic information systems (GISs) are systems of computer hardware and software that were developed to apply computational power to the tasks of cartographic modelling. In particular, GISs make it easier to manage multiple layers of data over large regions. Comprehensive overviews of GIS technology are available in Antennucci and Planagraphics (1991), Aronoff (1989), Ashdown and Schaller (1990), Bracken and Webster (1990), Burrough (1986), Clarke (1990), and Star and Estes (1990). A short history of the technology follows.\(^5\)

Most of the earliest work on GIS technology was done at the Harvard Laboratory for Computer Graphics where it was inspired by the cartographic modelling efforts of Steinitz and others (e.g., the IMGRID system). Initially, all GIS technology required the use of raster data in which the cells on a regularly and

\(^5\)This short history is based on Calkins and Tomlinson (1977), Chrisman (1988), Dangermond et al. (1982), and Star and Estes (1990, pp. 17-23).
perfectly tesselated surface would each be assigned a data value. Regular tessellations could be triangular, square, or hexagonal, but most systems adopted square cells. These provided the most straight-forward approach to developing hierarchies of tessellations (e.g., the quadtree system, see Peuquet 1991). The first fully functional raster GIS was the Canadian Geographic Information System (CGIS) initiated in 1964.

Raster systems proved to be confining especially to the extent that data was lost to the reduced resolution of a gridded surface, so several attempts were made to develop GISs using pure cartographic objects (points, lines, and polygons). Such systems are referred to as vector systems. Vector systems may use one of two basic organizational principles. The "spaghetti" system is one in which points and lines are pure digitized objects and arcs and polygons are simply aggregates of line segments. The topological system is one in which points, segments, and arcs have information stored for adjoining points, segments, arcs, and polygons (Peuquet 1991). The first vector-based system (PIOS) was developed by Jack Dangermond, founder of the Environmental Systems Research Institute. PIOS has now evolved into Arc-Info, the best selling vector-based system.

Today, many hybrid GIS systems are on the market. Most of these include both raster and vector formats, complex spatial statistics, map overlays, and map algebra options. Some include topological information options. Small GISs capable of running on a micro-computer include ARC-INFO for the PC, OSU-MAP, and
Idrisi (Marble and Amundson 1988). Idrisi (Eastman 1987-1992) is an inexpensive, simple GIS that includes both raster and vector options, numerous options for data analysis, and, beginning with version 4.0 in 1992, topology. It is an excellent tool for cartographic modelling, and was used for the present study.

2.3.6 Spatial Description and Landscapes

The three basic processes of spatial analysis are description, classification, and combination of data for the purposes of explaining structure, function, and change at various spatial and temporal scales (Turner 1989a). Classification of ecotopes and the combination of data in general are discussed in earlier sections of this chapter. In the context of the landscape, descriptive processes are used to address questions about ecosystem functions; biological diversity; organism, nutrient, and energy flows between ecosystems; and landscape stability and change (Forman and Godron 1984, 1986).

Several workers have attempted to develop and propose standard approaches to landscape surveys (Christian and Steward 1968; Haase 1984; Rowe and Sheard 1981; Vink 1983, pp. 72-96). None has emerged as clearly superior or uniformly useful. However, certain tendencies are very strong. Landscape ecological surveys virtually always include choroplethic treatments of topographic, vegetation physiognomic, and substrate variables. These are the components of the ecotope and the variables of its classification.
Although the basic ecological units of the landscape are its ecotopes, many analysts prefer to work from descriptive analyses of smaller component units that characteristically have more concise spatial characteristics (e.g., firmer boundaries). These are the patch, matrix, node, corridor, and network, the primitives of the more traditional landscape geographers and ecologists (Forman 1982; Forman and Godron 1981, 1986). Ultimately, of course, in cartographic modelling and analysis, the fundamental units are the cartographic objects (points, lines, and polygons).

Regardless of the selected units, a number of indices are available for spatially describing them and their relationships (most of these indices are reviewed in Forman and Godron 1986; also see Baker 1989, Hagget 1983, Noss 1990). These include:

a. for individual objects, as appropriate: area, perimeter, and shape (Austin 1984; Forman and Godron 1986, p. 188; Game 1980; LaGro 1991; Loehle 1991; Longley and Batty 1989; Patton 1975; Rex and Malanson 1990; Selkirk 1982, pp. 53-57; Turner 1989a);

1990), rank-size relationships (Isard 1956, Sullivan and Shaffer 1975), and heterogeneity (Forman and Godron 1986, pp. 222-225);

c. spatial measures for groups of objects: dispersion (nearest neighbor statistic) (Clark and Evans 1954, King 1969, Ripple et al. 1991), isolation (King 1969), accessibility (Lowe and Moryadas 1975), and interaction (Forman and Godron 1986, pp. 420-421; McDonnell 1984; Stewart 1947; Sullivan and Shaffer 1975; Whitcomb 1977); and

2.4 Selection and Design of Individual Nature Reserves

2.4.1 Species Considerations

The selection of species for conservation should emphasize those that are rare throughout their ranges, especially when ranges are limited, as with narrow endemics (Kruckeberg and Rabinowitz 1985), but it should also include peripheral and disjunct populations of species that are locally rare (Jenkins 1981). Disjunct populations that are reproductively isolated contain unique genetic material (Brown and Gibson 1983, Kruckeberg and Rabinowitz 1985, Slatkin 1987). The determination of rarity for species is scale dependent, based on information about spatial distribution and local abundance (Jenkins 1977, 1985).
Generally, species are best conserved in situ in populations large enough to be stable in ecological time and to maintain sufficient genetic variety to adapt to changing environments in evolutionary time. Frankel and Soulé (1981) refer to this as the minimum viable population (MVP) hypothesis. Few species can be conserved over the long term if their effective (actively reproducing) population levels ($N_e$) fall to the point that they begin to lose heterozygosity (heterosis).

The argument was first advanced by Soulé (1980) in his revolutionary article "Thresholds for Survival: Maintaining Fitness and Evolutionary Potential." This was followed quickly by a text by Frankel and Soulé (1981) and three very important symposium volumes (Schonewald-Cox et al. 1983, Soulé 1986a, Soulé 1987).

Based on domestic animal breeding data, Soulé (1980) and his successors estimated that the minimum viable population for most animals must be about 50 actively reproducing adults in order to keep inbreeding below 1% per generation to avoid the loss of heterosis. They increased this number by an order of magnitude to 500 in order to minimize genetic drift and to provide a margin of error (Lehmkuhl 1984).

$$MVP = N_e = 50-500$$

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Other perils of small populations include demographic and social dysfunctions (Wilcove 1987).
How reliable is the 50/500 rule? Various techniques for determining $N_e$ have been published in the literature, but most are extremely sensitive to original assumptions and measurements (Harris and Allendorf 1989, Kinnaird and O'Brian 1991, Simberloff 1988).

Even if $N_e$ is known reliably, its translation into MVP is problematic. For example, Belovsky determined that MVP varies inversely with body size. Given a criterion of 95% probability of persistence over 100 years, shrews (10 g) have an MVP on the order of $10^5$, rabbits ($10^3$ g) have an MVP on the order of $10^4$, and elephants ($10^7$ g) have an MVP on the order of $10^3$. Hubbell and Foster (1986) estimated that the MVP for tropical rain forest trees is about 60 adults per km$^2$. Density dependence (as is often the case with plants) results in inbreeding at higher population levels (Ginzburg et al. 1990). In a study that corroborated the 50/500 rule, Berger (1990), based on tracking records of bighorn sheep, reported that all populations of $N_e = 50$ or fewer sheep went extinct within fifty years of reaching that population level. Populations of up to $N_e = 100$ persisted for no more than 70 years.

Ewens et al. (1987) argued that for any given population, MVP for the persistence of heterosis is considerably higher than MVP for survival. The onset of inbreeding depression is considered to be universal with the loss of heterosis, but the extent of its impact is highly variable (Ralls et al. 1986). Lacy (1992) studied extinction among populations of mice. His initial expectation was that inbreeding
would produce less depression of fitness (measured as infant mortality) in isolated, small populations with a long history of inbreeding than in large, central populations. In fact, the loss of fitness did not correspond significantly with initial heterosis, size, or isolation.

What exactly is the effect of homozygosity on a surviving population? Studies of inbreeding depression in the strongly homozygous cheetah documented the loss of reproductive capacity (sperm aberrations and high infant mortality), yet the cheetah population appears to be relatively stable in the absence of human interference (O'Brien et al. 1983, 1985). Similar effects were documented for red and torrey pine, both obligate out-breeding trees with low heterosis (Ledig 1986). On the other hand, Bonnell and Selander (1974) report on the recovery of elephant seals from about 20 homozygous adults to 30,000 adults in 75 years. Both Templeton (1986) and Thomas (1990) discussed several instances of rapid recovery or persistence for many years of homozygous populations. Of course, homozygous survival begs the question of evolutionary adaptability, unless heterosis can be recovered.

Lacy (1987) and Boeklen (1986) report on the basis of computer simulations that genetic drift is the overriding factor in the loss of genetic variation in small populations. In Lacy’s experiments, natural selection failed to counter genetic drift in isolated populations of MVP less than 100 over 100 generations, but tiny amounts of immigration between populations slowed, halted, or even reversed the loss of
heterosis. Both researchers also expect that while subdivided populations without immigration will rapidly lose internal variation, they will preserve more total variation than a single large population (also see Drury 1974).

Maguire (1986, 1991; et al. 1987) and Starfield and Herr (1991) provide guidelines for using the calculated risks of extinction associated with low \( N_e \) to make decisions about environmental management (e.g., nature reserve design), but there really is no way to know when \( N_e \) is too small for any given species other than to measure the loss of heterosis and its putative effects. Shaffer (1987) considers estimations of MVP to be highly uncertain, and recommends large, cautious adjustments upward from the 50/500 rule.

It is essential to design nature reserves and networks of reserves to conserve the rarest and most threatened species. On the other hand, it is almost impossible to estimate whether such reserves and networks will be successful based on evaluations of minimum viable populations. Instead, species conservation efforts should focus on capturing potentially stable portions of the landscape including ecotopes that provide habitat for target species.

2.4.2 Ecosystem Considerations

Many authors have summarized the various criteria that agencies use in the process of selecting and designing individual nature reserves (e.g., MacKinnon, et al.
1986, Margules and Usher 1981, McNeely 1988, Salm and Clark 1984, Smith and Theberge 1986). Typical criteria include species or ecosystem rarity and ecosystem uniqueness, size, shape, naturalness, productivity, fragility, representativeness, habitat values, threat, educational value, recorded history, research investment, scientific value, recreational value, and various management considerations (e.g., consideration of buffers or boundaries, accessibility, defensibility).

When applying these criteria to ecosystems, it is useful to realize that some criteria are more applicable at certain levels than at others. A general rule-of-thumb is that criteria for conservation are best applied at or below the level in the ecosystem classification where the conservation criterion variables are directly addressable based on the ecosystem classification variables. For example, conservation criteria based on species typically should be applied at or below the level of the ecosystem classification where species are included in the ecosystem description.

The workshop on ecosystem classification and conservation held at the East-West Center in 1991 developed a list of criteria for evaluating ecosystem occurrences for conservation (Pearsall 1991c).

2.4.2.1 Diversity of Species

Diversity of native species is a relative measure of the complexity of the ecosystem. For some terrestrial ecotopes (e.g., rain forests) this diversity may be a
very useful criterion for selection. It is not useful for many, perhaps most, other ecosystems such as grasslands, caves, vegetated wetlands, sparsely vegetated ecosystems, marine ecosystems, mangroves, etc.

Diversity of endemic species is a very good measure of the distinctiveness of the ecosystem type. Where the goal is conservation of genetic diversity, ecosystems with high endemic diversity are valued more highly. It is useful to distinguish among the forms of endemism. In the case of relict endemism, the endemic species was once more widely distributed, and there is some probability that the relict species is naturally approaching extinction at the end of the taxon cycle (Ricklefs and Cox 1972, Wilson 1961). In the case of autochthonous endemism, the species evolved where it is now found. High diversity of autochthonous species is an indication that the local environment is a productive context for the evolution of new species. This criterion has particular relevance for the supra-littoral ecosystems of oceanic islands, where the majority of species (especially plants, invertebrates, and birds) are typically autochthonous endemics.

Priority should be given areas with high diversity of rare species. Rabinowitz (1981) and others have defined several different kinds of natural species rarity. Generally these can be lumped together in the following way (in approximate order of conservation priority):
a. species that are rare across large ranges (e.g., many predators, whales, marine turtles)

b. species that are rare because their ranges are small (endemic species, see above)

c. species that are rare as an artifact of the observer's spatial or temporal references or limits (e.g., a species that is classified as rare in one country although it is common in another country)

Note that narrowness of niche can exacerbate rarity for any of these classes.

Sites for threatened species should also be given high priority. Species may be threatened by ecosystem deterioration or excessive predation (e.g., by humans). Ecosystems including species that are both rare and threatened should be given higher priority than ecosystems providing habitat for rare but non-threatened species. Two examples of the latter would be wide-ranging species that are rare as the result of an adaptive strategy (top predators) and species that are rare because they are specialized to rare but non-threatened ecosystems, even though they are locally quite common (e.g., endemic plants in the cloud forests of high islands).

2.4.2.2 Critical Habitat

In the previous section, ecosystem-level diversity of rare or threatened species was presented as a criterion for conservation. It may be that an ecosystem is not rich in rare species, but that it provides critical habitat for individual species that are rare

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and/or threatened. In this case, the conservation priority of the ecosystem would be vary with the conservation priority of the rare or endangered species.

Refugia are places where species or whole suites of species may survive as generations of individuals or as seeds during times of natural or human induced environmental stress. Former, current, and potential refugia would all have conservation priority. The environmental stresses against which relatively undisturbed, unmanaged, native ecosystems provide the best refuges are the long term, natural or human-induced, global, atmospheric fluxes (e.g., climate change). Other refugia, those that are more intensively managed and/or those that are less natural (more disturbed or non-native), offer some protection from short term changes in the environment, but are unlikely to persist over cycles of global change.

2.4.2.3 Ecosystem Rarity, Distinctiveness, Resilience, and Threat

Ecosystem types that are rare would have relatively more priority than ecosystem types that are common. Again, if rarity is the product of environmental deterioration or direct destruction, the ecosystem would be considered threatened, and given higher priority than if the ecosystem is rare but not threatened, e.g., if its soil and/or climatic requirements are rare, but its occurrences are secure. Highest priority would be given to ecosystems that are both rare and threatened.
The distinctiveness of an ecosystem type may have much to do with the inclinations of the classifying scientist to lump or split types. Even so, the workshop assigned higher priority to more distinctive ecosystem types based on species composition, distinctiveness of the soil substrate, and distinctiveness of ecosystem patterns and processes (e.g., the Pisonia - seabird excrement interactions that produce phosphates under atoll forest soils).

The workshop considered ecosystem resilience in particular (to particular disturbances) or in general (to whole classes of disturbances) to be a useful conservation variable. Less resilient (more fragile) ecosystems are expected to attract the attention of those agencies most inclined to invest in higher risk, more strictly protected reserves (e.g., private and international conservation organizations). More resilient ecosystems will attract the attention of agencies that are less inclined to take risks and more inclined to permit or encourage multiple human uses of the reserves (e.g., government agencies).

Ecosystem types that are known to be threatened will usually receive higher priority for conservation than those that are not known to be threatened. Human threats to ecosystems hardly need elaboration. In addition to removing, modifying, or destroying ecosystems during land-use changes or as a result of pollution, and in addition to causing general, perhaps global, environmental flux, humans introduce non-native species and fire to otherwise undisturbed native ecosystems. Some
ecosystems cope reasonably well with these introductions. In fact some ecosystems are well adapted to invasions (even of non-native species), pollution, and/or fire. Others clearly are not.

2.4.2.4 Interdependence with Other Ecosystems

Ecotopes are open systems that are spatially and functionally interrelated with other ecotopes in the landscape. If an ecosystem strongly interacts with another ecosystem, the system of the two should be given higher priority for conservation than either ecosystem alone. If an ecosystem strongly interacts with another ecosystem that is considered important for conservation, then it too must be conserved, or it is likely that conservation efforts on behalf of the second will fail. In general, the higher the level of ecosystem interaction, the higher the conservation priority.

2.4.2.5 Questions of Minimum Size

Natural disturbances occur on a wide variety of temporal and spatial scales. They occur at different levels hierarchically, in fluctuating regimes that vary within and across landscapes and that overlay environmental gradients, sometimes in unpredictable ways. In other words, disturbances are essentially random (Botkin 1990, Holling 1973). Disturbance contributes to the variability and diversity of ecosystems (Loucks 1970, White 1987). Several authors have argued that for an ecosystem reserve to be stable, it must be large enough to accommodate the patch
dynamics of its component ecosystems without simplification or collapse (Foster 1980, Pickett and Thompson 1978, Russell 1987, Shugart and West 1981, Strong 1977, White 1987). Shugart and West (1981) used the FORET computerized forest simulation model to predict that the land area for a stable temperate forest must be 50 times the mean patch size.

Other size considerations include the provision of habitat or habitat components for all species (regardless of rarity) that play significant roles in ecosystem functions (e.g., fruit bats that pollinate flowers and disperse seeds). These must be maintained at populations sufficiently large to fill ecosystem roles (Addicott 1984, Billings 1983, May and Seger 1986, Southwood 1988, Wilson 1987). Finally, the ecosystem must be large enough to continue to play its role in landscape (inter-ecosystem) processes at a sufficient level to prevent the collapse of any associated ecosystems.

2.4.2.6 Representativeness

In the last decade it has become apparent that protected areas alone are insufficient for the conservation of biological diversity (Grumbine 1990, Newmark 1985). Protected areas must be selected, designed, and spatially related so that the landscape itself meets the criteria of ecological stability and adaptability (including its component ecosystems and species) (Harris and Noss 1987; Noss 1983a, 1983b, 1987a, 1987c; Noss and Harris 1986; World National Parks Congress 1984).
Conserving a representative set of stable ecosystems as reserves in each landscape thus constitutes an essential early step (Austin and Margules 1986, Crumpacker et al. 1988).

One of the most widely recognized approaches to selecting representative reserves is the gap analysis system of Scott et al. (1988, 1989b, 1990). In gap analysis, GIS technology is used to overlay information about existing nature reserves, distributions of rare and threatened species, areas of high species diversity, and natural community (ecotope) occurrences to determine where and how reserve systems are inadequate, for example, where reserve systems fail to include representatives of all ecotopes, or fail to include areas of significant species diversity. Gap analysis has been adopted by the USDI Fish and Wildlife Service.

Although gap analysis is popular, it makes better use of GIS technology than it does of ecology. There is no intrinsic procedure for consistently classifying ecosystems within a hierarchy nor are there intrinsic methods for evaluating representativeness, other than simply searching for holes in the data. By way of contrast, DeVelice et al. (1988) present a cogent overview of a landscape-wide approach to ecosystem conservation in New Zealand using landscape gradient analysis for the evaluation of representativeness, and basing classification of ecotopes on vegetation structure and substrate.
2.4.3 Considerations of Insularity

Terborgh (1973) first proposed that the principles of island biogeography provided very important principles for nature reserve design, namely that reserves should be larger and rounder in order to succeed. His proposal was essentially ignored until several others made the same proposal again in 1975 (Diamond 1975, May 1975, Wilson and Willis 1975). Simberloff and Abele countered in 1976 and the application of the MacArthur and Wilson theory to reserve design became very controversial (Diamond et al. 1976, Simberloff 1982, Simberloff and Abele 1976, Whitcomb et al. 1981). In fact, the controversy extended into hundreds of articles in the literature and quite overshadowed the discussions about the merits of the theory itself.

Terborgh and his successors maintain that rounder reserves are better, partly because they reduce edge effects, but mainly because rounder reserves have fewer peninsulas, and by extrapolation from the equilibrium model, peninsulas should have fewer species near their outboard ends. Many authors argued that topologically complex reserves represented better targets for immigrating species or that shape was essentially neutral (Blouin and Connor 1985, Game 1980). Others found evidence that rounder reserves experienced lower rates of emigration (Stamps et al. 1987). Since immigration of species to and from a habitat island nature reserve is generally undesirable (invasive species should be excluded and target species should be included), rounder is now generally recognized as better.
The resolution of the size issue was not so easy. No one ever argued that a single small reserve is better than a single large reserve, but given constraints on time and resources, which is better, a single large reserve or several small reserves? This question, stimulated by the Simberloff and Abele article (1976) was the essence of the "Single Large or Several Small Reserves" (SLOSS) debate (e.g., Gilpin 1988, Gilpin and Diamond 1980, Jarvinen 1982, Lahti and Ranta 1985, Murphy and Wilcox 1986, Quinn and Hastings 1988). Shafer provides an excellent overview of equilibrium theory and the SLOSS debate (1990, pp. 11-38, 79-82, 93-94). Soulé and Simberloff (1986) correctly observe that the equilibrium theory of island biogeography is actually neutral on the subject.

Ultimately, the SLOSS debate is prolonged by confusion about geographic scales of purpose versus action. If the goal is to sample a region’s species diversity, then several small dispersed reserves will virtually always capture more species (Higgs 1981, Higgs and Usher 1980). If the goal is to capture those species that require reserves to survive (typically non-invasive, non-edge, native species that are rare by virtue of being threatened), then large reserves will be required. For example, Humphreys and Kitchner (1982) found that in Western Australia, several small reserves captured higher diversity of species surviving outside of reserves while single large reserves captured higher diversity of species not surviving outside of reserves.
Ultimately, the most reasonable conclusion that can be drawn is that reserves for species should be as large and round as possible, each containing adequate habitat for the minimum viable populations of all of its targeted (especially rare) species. This approach will capture the highest diversity of non-edge, native species. Fragmentation of contiguous reserves should be avoided except in emergencies (see the discussion below under corridors).

2.4.4 Boundaries, Buffers, and the Boundary Model

Traditionally, nature reserve boundary design was guided by short lists of inclusion requirements (MacKinnon et al. 1986, Theberge 1989, Zentilli 1977). More recently, reserve boundaries have been recognized as complex, dynamic entities that should be considered more carefully.

There will always be a zone of interaction between the protected area and the surrounding landscape (Forman and Godron 1986, Schonewald-Cox and Bayless 1986). The zone of interaction extending outside the reserve (the geographer's "influence field") includes, among other things, the spatial extent to which propagules successfully disperse out of the reserve and the area within which the microclimate is influenced (Forman and Godron 1986). In order to manage edge effects, some or all of the external zone of influence should be formalized and managed as a buffer zone extending into the adjacent landscape (Harris and Noss 1987, Oldfield 1988, Noss 1987a, Noss and Harris 1986, Schonewald-Cox and Bayless 1986, Van der Maarl
Buffers should be capable of absorbing certain permitted human activities (e.g., hunting and gathering, recreation, swidden agriculture) and reducing or eliminating the access of non-native species, pollution, and human encroachments into the core (MacKinnon et al. 1986, Oldfield 1988).

The boundaries between the external landscape and the buffer and between the buffer and the core reserve generate influence fields extending inward as well (zones of edge effects) (Forman and Godron 1986, Lovejoy et al. 1984, Schonewald-Cox and Bayless 1986). Inward extending zones must be managed more strictly than adjacent, outboard zones. A core area must be large enough so that, after accounting for edge effects, the remaining area is large enough to sustain its component ecosystems and species (Burgess and Sharpe 1981b, Forman and Godron 1986, Harris and Noss 1987, Lovejoy et al. 1984, Noss 1987a, Noss and Harris 1986, Schonewald-Cox and Bayless 1986). Laurance and Yensen (1990) provide a means of estimating core area given a measured edge function (equal to the measured, mean penetration of the reserve by edge effects), the area of the whole reserve, and the length of its perimeter.

Schonewald-Cox and Bayless (1986) and Schonewald-Cox (1988) developed a formal model of the field effects of boundaries within reserves, between reserves and buffers, and between buffers and the external environment. The administrative boundary is a filter for human activity and interaction with the ecosystem(s) of the reserve.
reserve. The natural edges are the ecotones. The generated edge (actually a gradient or zone) is formed by the interaction of organisms including people with the administrative boundary and natural ecotones. The generated gradient may serve as a corridor of habitat for new species, as a filter for people or other species (that is, sometimes as a buffer), and as a locus for certain activities. The boundary gradient will vary around its perimeter, and so must be segmented into management units. Unstable situations are most probable in boundary gradients that are steep or narrow. When the gradient intrudes into the core, it degenerates the reserve. The boundary model is the design analogue of a dynamic ecotone model.

2.4.5 Incorporating Restoration Lands into Buffer Lands

Ecosystem recovery, rehabilitation, and replacement are popular, relatively new applications of ecology, all generally included under the rubric of "restoration ecology" (Cairns 1986). The Society for Ecological Restoration is well established. Restoration and Management Notes (Arboretum, University of Wisconsin at Madison) has been in publication since the early 1980s, and Restoration Ecology (Blackwell Scientific) is a new journal scheduled to begin publication in 1993.

Various authors differentiate between recovery, rehabilitation, and replacement (e.g., Cairns 1986). Recovery is the regeneration, presumably with some human assistance, of native ecosystems via succession (MacMahon 1987). Ecosystem rehabilitation is usually a small-scale and cautious process of returning an ecosystem
to some functional level. Replacement is the human-planned and managed reestablishment of a native (pseudo-native?) ecosystem (Cairns 1986, Schiechtl 1980). Replacement has much in common with environmental engineering and is typically practiced on severely degraded lands such as the former sites of surface mines. Its development has been stimulated by laws requiring such restoration.

Bradshaw (1987a) called restoration ecology the "acid-test of ecological knowledge." He (Bradshaw 1983, 1987b) pointed out that successful restoration requires excellent knowledge of pre-disturbance ecosystem diversity, composition, structure, and function. Allen and Hoekstra (1987) and MacMahon (1987) added scale and hierarchical position and function to the list.

Unfortunately, there is very little evidence that ecosystem replacement ever results in the fully functional and populated, targeted, native ecosystem (Ewel 1987, Gore and Bryant 1988, Howell 1986, Lamoureux 1985, MacMahon 1987, Noss and Starnes 1985, Turner 1989b, Zedler 1988). Restoration of deteriorated substrates and elimination of non-native species prove to be especially difficult challenges. Rehabilitation and recovery seem to have more potential for success, although these processes do sometimes fail. Duffy and Meier (1992) report that 45 to 87 years after clear cutting, the herbaceous understories of "recovered," temperate, deciduous forests have not recovered. Fortunately, from the perspective of the ecological stable landscape, perfect ecosystem restoration is rarely necessary. If disturbed and
displaced ecosystems can be restored to a functional level, they may contribute to landscape resilience and persistence (Allen and Hoekstra 1987).

Everglades National Park in the United States provides an extraordinary example of post hoc ecosystem restoration efforts in response to the destabilization of an entire landscape. Lake Okeechobee, the Everglades, Big Cypress Swamp, and the surrounding landscape comprise a highly interactive system of ecotopes linked by the movement of water and animals. Many of these ecotopes have collapsed or are approaching collapse as these movements have been interrupted by piecemeal agricultural and urban development. Corrective action is under way in the form of rehabilitation and replacement programs. The expense is likely to be enormous (Hendrix and Morehead 1983, Kahn 1986, Mitchell 1986).

Generally, ecosystem restoration should be a high priority function of buffer lands, with the major emphasis on ecosystems that have a high probability of recovery. Ecosystem replacement should conform to the best available understanding of normal spatial relationships among ecosystems. To the extent that ecosystems can be put anywhere, they should be put in the right places.
2.5 Designing Networks of Nature Reserves

2.5.1 Conceptual Background

After reflecting on the nature of ecosystem interactions in the landscape, Forman (1987) made the case that treating individual ecosystems as isolates (intellectually, as planning units, as conservation units, etc.) rather than as components in a larger system is unethical if the ethical goal is to conserve their functionality. It is certainly impractical. It appears likely that a stable landscape will be characterized by the patchiness of human-developed and managed areas in the matrix of native ecosystems rather than the other way around. The following sections deal with the challenges of conserving landscapes as networks of functioning ecotopes.

2.5.2 Overview of Fragmentation as the Dominant Theme

Fragmentation is the subdivision of the landscape into smaller than normal patches by the development or enhancement of barriers to normal species movements (often including ecosystem displacement and/or the introduction of non-native species). Complete fragmentation is thus the opposite of normative connectivity among native ecosystems. Edge effects vary directly with the degree of fragmentation.

The nested scales of the landscape include nested scales of fragmentation, i.e., a single large fragment at one scale contains many smaller fragments at another scale.
(Lord and Norton 1990). In general, the impacts of spatial fragmentation of the landscape are poorly understood for ecosystems. They are much better understood for species, and in most cases, ecosystem impacts must be inferred from the cumulative impacts of fragmentation on their component species. As the scale of fragmentation increases linearly, the significance of fragmentation effects for individual organisms increases geometrically. The extent to which individual ecosystems can buffer fragmentation effects by absorbing the impacts on species (ecosystem persistence and resistance in the presence of simplification) is rarely known.

According to Wilcove (1987), the sources of species extinction due to fragmentation are:

a. the loss of species that were originally excluded from the fragments;

b. the loss of species that no longer find certain fragments to be acceptable habitat (based on size, contents, neighbors);

c. the loss of species that can reproduce in the reduced habitat but that cannot emigrate nor maintain viably large local populations; and

d. the loss of species due to secondary effects (ecological chain reactions, e.g., secondary extinctions, edge effects, and invasions by non-native species).
According to Lande (1987), even when the MVP of a species is present, and adequate habitat is available for it, if the landscape is too fragmented, the young of the species may die because they cannot find suitable new territories.

Lovejoy et al. (1983, 1984, 1986) showed that in newly fragmented Amazonian landscapes, fragments of 10 ha or smaller had within a few days experienced marked changes in local temperature and humidity, and within 2 years experienced local extinctions of several species of birds and primates. These fragments were experiencing significantly higher levels of tree blow-downs, invasions of weedy species, and excessive predation on both animals and the unripe fruits of trees. Soulé (1986b) reports that fragmentation reduces the success of establishment and migration of species and of individual searches for episodic habitat events (e.g., flowering or fruiting).

Lord and Norton (1990) provided a useful overview of four significant, highly inter-dependent effects of fragmentation on landscapes. These are reduced fragment size, increased edge effects, increased isolation, and increased exposure and vulnerability to extrinsic influences. In an excellent review article, Sanders et al. (1991) discussed the emergence of the fragmented landscape and its characteristics. For example, for the non-biotic portion of the landscape, fragmentation results in increased albedo, higher fluxes of radiation at ground levels, higher re-radiation and cooler temperatures at night, lower humidity, and higher momentum for fluid
movement. Higher wind velocities and more lateral exposure increase tree blow-downs, seed dispersal, and dehydration (e.g., during a cyclone). Increased water velocities result in increases in erosion and nutrient transport. Plant gas exchange and access to sunlight will increase. Plant responses to these variables depend on the species. Other biotic changes include change in soil biota (to those of a warmer, drier regime), change from core to edge species, and the reduction (relaxation) of biota. This last may be aperiodic and chaotic instead of logarithmic as MacArthur and Wilson (1967) predicted. Diversity may drop to asymptotic lows that result in the local extinction of core species. According to Forman (1987), increasing the fragmentation of the landscape will increase the speed and violence with which disturbance propagates through it.

2.5.3 Nodes, Corridors, and Networks: The Anti-fragmentation Strategy

2.5.3.1 Reserve Clusters

As discussed in preceding sections, larger preserves are better. However, it's irresponsible to overlook the necessity to protect smaller reserves for the last remaining bits of rare ecosystems or the last struggling populations of rare species. The international tendency is to develop complexes of small reserves in conjunction with one or more larger core reserves. Two significant programs for developing reserve complexes are the UNESCO Man and the Biosphere Reserve Program (Johnson et al. 1977, McCrone 1984) and The Nature Conservancy's Bioreserve Program (Jenkins 1989, Sawhill 1991).
2.5.3.2 Corridors: An Overview

Networks of nature reserves can be connected by corridors designed to allow species to range across the landscape and to move between protected areas. Corridors are probably the most controversial aspect of landscape-level planning for conservation. Dendy (1987) summarizes some of the various positions.

Most authors feel that corridors increase the effective size of populations and their habitats, maximize heterosis within populations by encouraging occasional inter-population immigration, facilitate recolonization, serve as linear reserves, and provide shelter for adjacent human activities (e.g., wind breaks) (Bennett 1990; Boecklen 1986; Burkey 1989; Dimowski and Kozakiewicz 1990; Erwin 1991; Fahrig and Merriam 1985; Forman 1983, 1990b; Harris 1988b; Harris and Gallagher 1989; Harris and Noss 1987; Helliwell 1976; Hobbs et al. 1990; MacClintock et al. 1977; Noss 1983a, 1987a, 1987b; Noss and Harris 1986; Simmons 1978; Slatkin 1987; Sullivan and Shaffer 1975; Wegner and Merriam 1979; van Selm 1988). Harris and Noss (1987), Noss (1987a), and Noss and Harris (1986) maintain that a network of reserves, buffers, and corridors can simulate large areas of habitat for wide-ranging species. Harris and Atkins (1991) even maintain that corridors can serve changing distributions of entire communities (e.g., following large scale environmental perturbations).
Other authors caution that corridors can facilitate the spread of wildfire, disease, and pests; serve as refuges for undesirable edge species by increasing the reserve edge; operate as predation sinks; and, worst of all, divert funds and energy from efforts to develop higher priority, higher quality reserves (Dobson and May 1986, Hansson 1988, Henein and Merriam 1990, Simberloff 1988, Simberloff and Cox 1987, Soule and Simberloff 1986, Stolzenburg 1991).

Most of these authors on both sides of the issue are reporting on feelings and hypotheses rather than on research. Many of the proponents of corridors base their positions on a very reasonable but general opposition to fragmentation. For example, Noss attempts to explain the issue thus:

Critics point out that conservationists have not proved that any of these corridor strategies will work - or more precisely, that the null hypothesis of no effect of corridors has not been proved false. But null hypotheses in ecology are not straightforward. In this instance, two alternative null hypotheses are possible: there is no effect of corridors; or there is no effect of fragmentation (that is, of eliminating natural corridors). ... the null hypothesis of no effect of fragmentation has been tested and falsified, repeatedly, in many parts of the world. Indeed, the effects of fragmentation can be devastating. In general, then, we can reject the null hypothesis of no effect of fragmentation and consider maintenance of habitat corridors a viable option for conservation. (1991, p. 36)

The logical problem with Noss's statement should be obvious! The two alternative null hypotheses are not logical opposites. Disproving one does not prove the other. The fact that the negative effects of fragmentation are extreme provides no support at all for the hypothesis that there are positive, anti-fragmentation effects of corridors.
There are, however, important studies that do indicate positive benefits from corridors. In 1977, MacClintock et al. reported on their studies of bird populations in Maryland forest tracts. Small patches had smaller forest bird populations than large patches, except that one small patch with a corridor to a much larger patch had populations approximating those of the larger patch. Fahrig and Merriam (1985) found that white-footed mice in isolated woodlots had lower growth rates than mice in connected woodlots. They attributed this finding to inbreeding depression. Lovejoy et al. (1986) found that as long as a 2 km corridor connected their 100 ha reserve to the forest mainland, both antbirds and army ant colonies persisted in the small reserve, but when the corridor was cut, both ants and birds disappeared. This last study is particularly persuasive.

2.5.3.3 Corridor Design Considerations

Noss (1991) made the point that corridors are semipermeable, that they are filters that allow some species to pass and not others. The grave danger is that corridors will be filters favoring edge or other opportunistic species and providing roads for these species into reserves. It is especially important that the field effect of the corridor terminus must not extend into the reserve further than the field effect of the reserve boundaries without the corridor.

This problem can be addressed through corridor design. With the very significant exception of the concern about budgeting resources, other objections to
corridors also can be addressed by incorporating minimum design standards, including corridor buffers. Unfortunately, the minimum adequate design standards for corridors are quite strenuous. What are "high quality" corridors?

Corridors should be as wide as possible and follow the lines of natural features (e.g., streams, valleys, ridges) (Dendy 1987). Corridors intended for the movement of interior species, the "strip corridors" of Forman and Godron (1986), must also be wide enough to sustain interior communities after accounting for edge effects (Forman and Godron 1986, Harris and Noss 1987, Helliwell 1976, Noss 1987a, Noss and Harris 1986). Several authors provide approaches for calculating the minimum width of corridors in order to avoid corridors that are all edge environment. Corridors must be designed to be wide enough to include a core strip for any core species that are expected to pass through them. Assuming that edge effects influencing forest birds extend into corridors for 500 m., a corridor must be over 1 km wide. It must be 2 km wide in order to have a core strip as wide as the sum of its edges. The opportunities for 2 km corridors will be rare. Pace (1991) even maintains that a corridor should be large enough to support the disturbance regime of its core ecosystems. If this position is accepted, then corridors must be much wider than 2 km.

In an excellent study, Henein and Merriam (1990) reviewed the effects of corridor design on metapopulations of white-footed mice. They found that:
a. patches reached by one or more low quality corridors (little or no non-edge interior) were more likely to experience local extinctions;
b. metapopulations with exclusively high quality corridors were larger than those with one or more low quality corridors;
c. the proportion of high to low quality corridors produced positively correlated changes in the size of the metapopulations;
d. the addition of a low quality corridor to a metapopulation surviving in patches previously connected only by high quality corridors resulted in a reduction of the metapopulation; and
e. when the number of connected patches was held constant, increasing the number of corridors did not increase the metapopulation (redundancy of connectivity was not useful).

Ideally then, a network should be connected by a parsimonious set of high quality corridors, provided that the corridors can be monitored, managed, and cut if necessary, and especially provided that investment in corridors does not preclude investment in core reserves.

2.5.3.4 Stream Corridors

A reserve network should also include riparian lands and wetlands, since these play critical roles in the landscape, and since streams are very significant vectors for environmental impacts (Harris and Noss 1987, Noss and Harris 1986). Stream
buffers can be considered to be a special case of corridors, and should be established as part of the network. In a discussion of the establishment of buffer strips as part of logging operations, Hamilton and King state that:

Although neither an optimum nor a minimum width can be set arbitrarily for buffer strips, it is recommended that a minimum width of 25 meters on each side of the stream be used as a guide for establishing buffer strips. At the same time, it must be realized that the necessary width will vary with steepness of the terrain, the nature of the undercover, the kind of soil, and the amount of timber to be removed. (1983, p. 150)

Gore and Bryant (1988) recommend 30 horizontal meters or 8 horizontal meters plus 0.6 m per 1% of slope, whichever is greater. Both of these recommendations are based on two assumptions. The first is that logging will take place, and the second is that the main impact to be avoided is the surface transport of materials into the stream. These numbers can only serve as guidelines, since a number of other variables must be considered. For example, the stream margins may not be currently forested, in which case the buffer becomes an area for the restoration of riparian ecosystems. Agricultural chemicals may constitute the main threat to the stream, in which case it may be advisable to restrict the use of agricultural chemicals from a much wider buffer than is maintained in (or restored to) riparian ecosystems (to protect the buffer itself) (Lowrance et al. 1984). In general, if the goal is to conserve the stream ecosystem, it should be treated as the core ecosystem of a corridor and buffered adequately against edge effects. This provides a much more ambitious and difficult goal than merely the protection of water quality, and corridor width will reflect it.
2.5.4 Optimizing the Network for Agro-ecosystems and Customary Land Tenure

Pimentel et al. (1992) made the point that much of the biological diversity of typical landscapes is not resident in native ecosystems, but instead is characteristic of human agroecosystems. This includes many insects, edge species, adapted and domestic species, and cultivars. They also made the point that humans must occupy landscapes, and they urged the development of approaches to conservation that will not overlook these realities.

Many authors have written about the necessity to avoid taking land away from its customary holders and users, especially in places where people are dependent on land for their subsistence. A workshop on the conservation of biological diversity on customary lands was held by the South Pacific Regional Environment Programme in 1988 (Thomas 1989). That workshop concluded that the alienation of customary lands should be regarded as a last resort in the effort to conserve biological diversity.

The best approach to optimizing the network of reserves, buffers, and corridors for this limited suite of secular values is to adopt a few rules-of-thumb. Without sacrificing the incorporation of any rare or threatened ecosystems in the reserves network, avoid, when possible, the best agricultural land, whether or not it is already in agriculture, especially if it is customary land. Exceptions typically will be necessary for very high priority ecosystems. For all customary land that must be included in the network, seek non-alienation approaches to conservation, perhaps
through the use of economic incentives or alternative approaches to generating income (McNeely 1988, Thomas 1989).
CHAPTER 3

FOUNDATION DATA AND A GEOGRAPHIC INFORMATION SYSTEM

3.1 Mapping the Vegetation of Western Samoa

Various types of natural resources data were identified as available for Western Samoa. However, no good vegetation data were available except for a few articles dealing with the highest elevations of Savai'i and the Aleipata Islands (Whistler 1978, 1983a) and a poorly mapped forest inventory, restricted to areas of native timber extant in 1978 (Olsen and Co. 1978). Thus, the most pressing need was for vegetation data covering the whole country at a consistent scale. The first step in this research was to map the terrestrial vegetation of Western Samoa.

3.1.1 Classification of Vegetation

The implementation of any inventory requires the definition of the class of objects to be inventoried. In this case, a classification of terrestrial vegetation was prepared based on several published and unpublished works (Amerson et al. 1982a, 1982b; Dahl 1980; Estes, Fosberg 1957; Holloway and Floyd 1975; Ollier et al. 1979; Olsen and Co. 1978; Uhe 1974; Whistler 1976, 1978, 1980, 1983a, 1983b, 1984, 1990; Wright 1963), and on extensive personal communications with experts such as Fosberg and Whistler from 1987 to 1992. The classification was based on vegetation formations, with further provision for associations as sub-classes, and thus was potentially hierarchical following the model established by the Honolulu Expert
Workshop on Ecosystem Classification. The following outline summarizes the organization of the classification. Map units are underlined:

I. Terrestrial Environments (majority of nutrients from soil)
   A. Hydric (wet)
      1. Swamp Forest
      2. Herbaceous Marsh
      3. Mangrove
   B. Mesic (moist)
      1. Coastal Rain Forest
      2. Lowland Rain Forest
      3. Ridge Rain Forest
      4. Fernland
      5. Montane Rain Forest
      6. Cloud Forest
   C. Xeric (dry)
      1. Grassland
      2. Volcanic Succession
   D. Littoral (xeric/halic; generally dry, salt influenced)
      1. Littoral Scrub
      2. Littoral Shrubland
      3. Littoral Forest

II. Aquatic, Marine, and Subterranean Environments (not included in this study)

The hierarchical outline includes only primary native vegetation, defined for the purposes of this work as vegetation that is:

a. dominated by native species, or rarely, Polynesian introductions; and
b. in successional steady-state, i.e., vegetation where, in the absence of invasion by non-native species, the patch dynamic does not produce a change in the overall species composition of the cover synusia (layer).
Only one secondary native vegetation type was mapped. This was Secondary Mesic Forest, a category that includes the late successional seres of Coastal, Lowland, and Montane Rain Forests. Early successional species in these forests are essentially the same. Other vegetation types are considered to be auto-successional. Secondary Mesic Forest is not included in the previous classification outline, but it was described and mapped when the sites were large enough.

The classification evolved considerably during the course of the mapping project based on interpretation of aerial photography of Western Samoa (New Zealand Aerial Mapping, Ltd. 1981, 1987), interpretation of a SPOT Satellite image of Western Savai’i, and eight weeks of field research in Western Samoa with which Dr. Arthur Whistler assisted.

3.1.2 Vegetation of Western Samoa

3.1.2.1 Cloud Forest (Vegetation Code: CF)

Species that may be locally dominant include Reynoldsia lanutoensis, Reynoldsia pleiosperma, Spiraeanthemum samoense, and Syzygium samoense. Cloud Forest is a low forest or sometimes a low woodland with many epiphytes (mostly mosses and ferns) and climbers, dense ground cover (mostly mosses and ferns), and

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Although various references are cited for each vegetation type, with the exception of the highest elevation types, these descriptions are based primarily on field observations (Pearsall and Whistler 1989). The list is in alphabetical order by map code. These descriptions are modified from those appearing in Pearsall and Whistler 1991a, pp. 73-86.
few lianas. It is generally found above 1200 m elevation, and is considered the wettest of Samoa’s forests. In parts of its range, this wet forest is misnamed in that the majority of moisture comes from precipitation rather than from the capture of cloud moisture by vegetation. However, all high elevation wet forests composed of the same species as the true Cloud Forests reasonably can be lumped together under that name. Spiraeanthemum and Reynoldsia are the most common dominants. Reynoldsia may be used as an indicator species for the transition from montane rain forest, while Spiraeanthemum is dominant at higher elevations. Syzygium dominance is rare. Cyathea patches are maintained in the primary forest by the patch dynamic. This is a rare vegetation in terms of number of occurrences, but these are all contiguous on the crest of Savai’i where they are undisturbed and essentially non-threatened. References include Dahl (1980), Olsen and Co. (1978), and Whistler (1978, 1980).

3.1.2.2 Coastal Rain Forest (Vegetation Code: CR)

Species that may be locally dominant include Diospyros elliptica, Diospyros samoensis, Syzygium clusiifolium, and Syzygium dealatum. Coastal rain forest is an uncommon vegetation type sometimes found between the littoral and lowland forests. It supports little ground cover and few epiphytes or lianas, but climbers are common. It is generally found on steep rocky coastal slopes and small offshore islands formed from tuff cones, and it sometimes invades old coconut plantations. Some of the few remaining occurrences are severely disturbed, but most are relatively undisturbed on

3.1.2.3 Fernland (Vegetation Code: FL)

*Dicranopteris linearis* is the dominant species. The fernland vegetation type is found as inclusions in the Ridge Rain Forest. It is found primarily on burned over coastal ridges on eroded soils of highly weathered volcanic clays with relatively low pH. This native disclimax vegetation is maintained by landslips (as in hurricane Ofa) and now by fires set by people. References include Dahl (1980) and Whistler (1980).

3.1.2.4 Grassland (Vegetation Code: GL)

*Imperata conferta* is the dominant species. This very rare native vegetation (one occurrence) is found only on ash plains in the highlands of Savai’i as an edaphic disclimax. References include Dahl (1980) and Whistler (1978).

3.1.2.5 Herbaceous Marsh (Vegetation Code: HM)

Species that may be locally dominant include *Acrostichum aureum, Carex graeffeana, Carex maculata, Cyclosorus interruptus, Eleocharis dulcis, Paspalum conjugatum, Paspalum orbiculare, Rhynchospora corymbosa,* and (rarely) *Scirpodendron ghaeri.* Eleocharis tends to be dominant in poorly drained coastal lowlands, while *Carex* or *Paspalum orbiculare* tends to be dominant in crater marshes and poorly drained upland sites above 1200 m elevation. Both occur on saturated
soils. None of the HM dominants except *Acrostichum* tolerates salt water. During hurricane Ofa in 1990, many Herbaceous Marshes on northern and eastern shores were poisoned by salt water incursions. *Rhynchospora* is a good indicator of disturbance. *Cyclosorus* may be a good indicator of relatively undisturbed coastal marshes. *Ludwigia octovalvis*, an alien species and an indicator of disturbance, is common around the edges of otherwise undisturbed coastal marshes. References include Dahl (1980), Ollier et al. (1979), and Whistler (1976, 1980).

3.1.2.6 Littoral Forest  (Vegetation Code: LF)

Species that may be locally dominant include *Barringtonia asiatica*, *Calophyllum inophyllum*, *Hernandia nymphaeifolia*, *Pisonia grandis*, and *Terminalia catappa*. Although the Littoral Forest is generally a mixed-dominants vegetation type, *Barringtonia* sometimes forms single species stands with dense canopies and open floor. Less frequently, *Pisonia*, *Calophyllum*, or *Hernandia* is locally dominant. The seaward margin of this community may be wind and salt stunted or pruned, and thus of approximately the same height as the Littoral Shrub or Scrub. In this case, the species may mix and the transition from Littoral Shrub or Scrub to Littoral Forest may be quite gradual. The inland transition to coastal or lowland forest usually is abrupt. This forest supports few epiphytes, lianas, or climbers, and ground cover is generally sparse. Littoral Forest may invade old coconut plantations along the shore. Most Littoral species are propagated by seeds that float and are impervious to salt water or that are sticky and thus transported by sea birds. The distributions of most

3.1.2.7 Littoral Scrub (Vegetation Code: LP)

**Pandanus tectorius** is the dominant species. This vegetation is found on relatively young lava flows along basaltic coasts between the rock strand and the littoral forest. This vegetation is typically subject to extreme wind shear, high salt conditions, and very low precipitation. When undisturbed, ground cover is sparse, and epiphytes and climbers are rare. Lianas are not found in this community. **Pandanus** in favorable situations often forms mono-specific stands. This vegetation is rare, and found in mappable stands only on the south shore of 'Upolu. References include Dahl (1980), Ollier et al. (1979), and Whistler (1980).

3.1.2.8 Lowland Rain Forest (Vegetation Code: LR)

Species that may be locally dominant include **Dysoxylum maota**, **Dysoxylum samoense**, **Intsia bijuga**, **Planchonella torricellensis**, and **Pometia pinnata**. This formerly widespread vegetation type occurs on coastal alluvial deposits and stream valleys, on talus slopes, and on lowland basalts. **Pometia** and **Dysoxylum** tend to occupy the lower sites, and good stands of these Lowland Rain Forests are now rare and typically confined to rocky and/or steep sites with poor soils. **Planchonella** tends to occupy higher sites, and **Planchonella**-dominated sites, including those on better soils, are more common. **Intsia bijuga** is a highly prized tree for canoe building, and
Intsia dominated sites are now very rare. It is important to note that dominance in this forest must be measured, as all five potential dominants are usually present in any occurrence of the vegetation. Many of the remaining sites are disturbed, but good examples of this vegetation are not as rare as expected. This community is Samoa's only stratified forest. It has moderate to heavy ground cover, and many epiphytes, lianas, and climbers. Lowland Rain Forest is generally found below 350 m elevation. 

**Rhus taitensis** patches are maintained in the primary forest by the patch dynamic. Major indicators of disturbance include **Macaranga** spp. and the alien species **Albizia chinensis** (emergent from the canopy in the hills south of Apia, maintained by the patch dynamic), **Castilloa elastica** (a canopy tree maintained by the patch dynamic), and **Funtumia elastica**, which does well in shade and may completely dominate the understory. References include Dahl (1980), Olsen and Co. (1978), and Whistler (1980, 1983a).

3.1.2.9 Littoral Shrubland (Vegetation Code: LS)

Species that may be locally dominant include **Dendrolobium umbellatum**, **Scaevola sericea**, and **Wollastonia biflora**. Littoral shrubland is a widespread but uncommon vegetation type in the littoral zone, usually found on the seaward margins of Littoral Forest or Scrub or Coastal Rain Forest. It is subject to salt spray, high winds and temperatures, and little precipitation. **Scaevola** is the most common dominant. Most Littoral species are propagated by seeds that float and are impervious to salt water or that are sticky and thus transported by sea birds. The
distributions of most Littoral species span the Indo-Pacific region. References include Dahl (1980), Ollier et al. (1979), and Whistler (1980).

3.1.2.10 Mangrove (Vegetation Code: MG)

Species that may be locally dominant include Bruguiera gymnorrhiza, Rhizophora mangle, and Xylocarpus moluccensis. There is only one occurrence of Xylocarpus in Western Samoa. Mangroves are found on brackish water sites along the coast where there is off-shore protection from wave action. Rhizophora tends to be locally dominant on disturbed sites, on mud substrate, and along the seaward margins of undisturbed sites. The Rhizophora component is shrubby, rarely more than 3 m high. Rhizophora is an obligative halophyte. Bruguiera tends to be dominant inside the Rhizophora band at somewhat higher elevations and in less salty water, on undisturbed sites, along tidal inlets with good circulation, and on sandy bottoms. Bruguiera is a facultative halophyte and is often present, though rarely dominant, in inland, lowland swamps. Bruguiera may support some epiphytes, especially ferns. There are no climbers or lianas and ground cover is absent. The Xylocarpus dominated occurrence is found on white sand. A single occurrence may include both Bruguiera and Rhizophora components, but these will be found in virtually mono-specific bands based on the substrate. References include Dahl (1980) and Whistler (1976, 1980).
3.1.2.11 Montane Rain Forest (Vegetation Code: MR)

Species that may be locally dominant include *Calophyllum neo-ebudicum*, *Dysoxylum huntii*, *Metrosideros collina*, and *Syzygium samoense*. Montane rain forest is a common vegetation type under little conversion pressure. It supports many epiphytes, climbers, and lianas, and a thick ground cover. The Montane Rain Forest is the richest community (as measured by the number of component species) in Samoa. The majority of Samoa’s fern and orchid species are found in this type. It is not generally considered to be a stratified forest, but several species, including *Heliconia paka*, *Angiopteris evecta* (king fern), and *Cyathea* spp., comprise a patchy, partial stratum at about two meters. *Metrosideros* dominated sites are extremely rare, and only one such was mapped in Western Samoa. There is a broad transition from Lowland and Ridge Rain Forests to the Montane Rain Forest, and in this transition, *Calophyllum* may be locally dominant. Generally, the Montane Rain Forest can be said to begin where one of the Montane Rain Forest dominants, usually *Dysoxylum huntii*, becomes more locally abundant than any one of the Lowland Rain Forest dominants. The Montane Rain Forest occupies a broad elevation band from as low as 300 m to as high as 1,200 m. *Cyathea* and *Musa* spp. are indicators of disturbance. *Cyathea* is locally dominant as a disclimax on steep valley walls. *Rhus taitensis* patches are maintained in the primary forest at lower elevations by the patch dynamic.

3.1.2.12 Ridge Rain Forest (Vegetation Code: RR)

Species that may be locally dominant include Canarium harveyi, Canarium vitiense, Planchonella garberi, and Syzygium inophylloides. Ridge Rain Forests generally occur on ridges of highly weathered, excessively drained, nutrient poor, volcanic soils. They support little ground cover and moderate numbers of epiphytes, lianas, and climbers. Elevation limits are typically 250-550 m. Landslips are quite common, and this vegetation type may be a disturbance-based, edaphic disclimax. This forest also is increasingly disturbed by fire or replaced by steep-slope, low-potential agriculture. Canarium dominated sites are rare. Rhus taitensis patches are sometimes present, maintained by the patch dynamic. Major indicators of disturbance include Macaranga spp. and the alien species Albizia chinensis (emergent, maintained by the patch dynamic) and Castilloa elastica (a canopy tree maintained by the patch dynamic). References include Dahl (1980), Ollier et al. (1979), Olsen and Co. (1978), and Whistler (1980).

3.1.2.13 Swamp Forest (Vegetation Code: SF)

Species that may be locally dominant include Barringtonia samoensis, Erythrina fusca, Hibiscus tiliaceus, Inocarpus fagifer, Kleinhovia hospita, Palaquium stehlinii, Pandanus turritus, and Terminalia richii. Pandanus turritus dominates an uncommon Swamp Forest vegetation in montane craters. Erythrina and Inocarpus are dominants, often in mono-specific stands, in uncommon, typically disturbed lowland and coastal Swamp Forests. Ground cover varies from dense to absent. This forest
supports few climbers or lianas but many epiphytes. There are very few large,
mixed, upland Swamp Forests on 'Upolu and none on Savai'i. Only one of these on
'Upolu is relatively undisturbed, and it is threatened. References include Dahl
(1980).

3.1.2.14 Secondary Forest (Vegetation Code: SM)

Species that may be locally dominant include Cyathea spp., Dysoxylum
samoense, Elattostachys falcata, Fagraea berteroana, Hibiscus tiliaceus, Inocarpus
fagifer, Kleinhovia hospita, Macaranga harveyana, Musa x paradisica var. seminifera,
Omalanthus nutans, Rhus taitensis, and Trema cannabina. Secondary Forest, as a
distinct vegetation type, is the secondary successional forest that is transitional to
mature rain forests (Coastal, Lowland, Ridge, and Montane). Essentially the same
species are found in each case. Musa is restricted to higher elevations, and at lower
elevations Dysoxylum samoense tends to be an early dominant. At all elevations
below the Cloud Forest, Rhus taitensis is a common dominant (often in single species
stands). In early stages, climbers and ground cover are abundant, and lianas and
epiphytes are sparse. Later, lianas and epiphytes are abundant, climbers less

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2In the case of secondary succession, Rain Forests are the only vegetation types in
Samoa that follow earlier successional stages that include markedly different species
associations. All others are auto-successional, a common characteristic of island
vegetation. Thus, secondary littoral and wetland vegetation, for two examples, were
not defined or mapped. Primary succession, as on lava flows; disclimax situations, as
on steep slopes; and patch dynamic vegetation are all discussed elsewhere.
abundant, and ground cover sparse. All Secondary Forest in Samoa is disturbed. References include Whistler (1980).

3.1.2.15 Volcanic Succession (Vegetation Code: VS)

Species that may be locally dominant include *Arytera* brackenridgei, *Coprosma strigulosa*, *Davallia solida*, *Fagraea beteroana*, *Glochidion ramiflorum*, *Metrosideros collina*, *Morinda citrifolia*, *Nephrolepis hirsutula*, *Spiraeanthemum samoense*, *Vaccinium whitmeei*, and *Weinmannia affinis*. Primary succession on inland lava flows and cinder cones results in this persistent, but nonetheless successional, vegetation. This successional process is characterized by early invasion of the lava or cinder surface by lichens and ferns; then by *Vaccinium* at higher elevations; then by seedlings of mainly *Arytera*, *Fagraea*, and *Glochidion* on lowland sites and of mainly *Coprosma*, *Metrosideros*, *Spiraeanthemum*, and *Weinmannia* on upland sites. These eventually grow into mature trees, scattered as woodland. *Morinda* is sometimes (but very rarely) dominant on small, lowland sites. Volcanic Succession is eventually replaced by Rain or Cloud Forest. Succession on fresh volcanics in the littoral zone is generally accomplished by littoral species already well adapted to arid, rocky environments and more tolerant of salt than the inland species that specialize in Volcanic Succession. Thus littoral volcanics are occupied by littoral vegetation from the outset of succession. References include Uhe (1974) and Whistler (1978).
3.1.3 Vegetation Mapping

3.1.3.1 Aerial Photography and Field Work

Aerial photographs of Western Samoa were provided by the South Pacific Regional Environment Programme (SPREP). These were 1:50,000 panchromatic photos taken in 1987, supplemented by 1:20,000 panchromatic photos from 1981 for the eastern ends of 'Upolu and Savai’i where cloud cover precluded the use of the 1987 photos (New Zealand Aerial Mapping 1981, 1987). These photos were stereoscopically inspected at one and ten power magnifications, and lines were drawn on acetate overlays around photomorphic regions (map units or areas of uniform texture) (Campbell 1987, pp. 98-99). The 1987 photos and their acetates were enlarged to a scale of 1:20,000 using a large format, flat-bed camera. Map units were then traced onto 1:20,000 topographic maps provided by the Samoan Department of Agriculture, Forests, and Fisheries (New Zealand Map Series 174). The process of tracing map units onto the maps required a certain amount of adjustment or "rubber-sheeting" to compensate for errors created by variations in the relative altitude of the airplane. Coastlines, roads, and volcanic peaks (in order of reliability) were used as references. Two precautions were taken to insure that the inventory would be scientifically honest: no attempt was made to develop correspondence between the traced map units and land-cover as shown on the existing topographic maps; and no attempt was made to classify map units prior to visiting them in the field.
In preparation for field verification of map units and identification of vegetation, information was assembled on the more common plant species in Western Samoa. This information was extracted from the literature (Christophersen 1935, 1938; Lloyd and Aiken; Parham 1972; Whistler 1983a, 1983b, 1984, 1990) and then extensively revised in the field (Appendix 4 in Pearsall and Whistler 1991a).

Whistler and Pearsall spent eight weeks in Western Samoa during July, August, November, and December 1989. During that time, most of the map units on Savai'i and 'Upolu were visited. Characteristic species were recorded for all lowland map units and the accessible upland map units on the two main islands. Visited map units were described, and most were photographed. The degree of and the agents of disturbance were also recorded for individual map units where appropriate.

Following tropical cyclone Ofa (February 1990), Pearsall spent two weeks in August 1990 revisiting all lowland map units and conducting remote surveillance of upland sites from passable roads. On this trip, the level and nature of damage were assessed. A second major tropical cyclone, Val, struck the islands in December 1991. No follow-up work on that cyclone was possible, and this research does not reflect any changes that occurred as the result of that storm.

Based on the field experience in July and August 1989 and on the literature, species descriptions and species and vegetation correspondence tables were prepared and indicator species were selected for individual vegetation types (Appendix 5 in
Pearsall and Whistler 1991a). These data were used extensively during the second round of field work in November and December 1989, when they proved very useful as a guide for determining vegetation. During both 1989 phases of the field work, the vegetation classification was itself extensively revised, and vegetation type descriptions were prepared.

3.1.3.2 Labeling Map Units and Managing Map Unit Data

Following completion of the 1989 field work, air photos for all map units were reevaluated under the stereoscope, based on notes and photographs from the field investigations, and using regional and topical references (Avery 1978, Campbell 1987, Lillesand and Kiefer 1979, Naval Photographic Interpretation Center 1950, USGS 1944). Map units were redrawn as needed, then all map units were traced onto draft velum overlays. Each map unit was labeled with basic location and classification codes (map code = Map Sheet Number: Map Unit Number: Vegetation Code) where the map sheet number was the New Zealand Map Series sheet number, the map unit number was a sequentially assigned number beginning with number 1 on each sheet, and the vegetation code was the two letter mnemonic for the vegetation type. The vegetation code was preceded by the letter "D" when sites were disturbed. Thus, 14:21:DHM would be the map code for Disturbed Herbaceous Marsh, mapped as the 21st map unit or polygon on map sheet 14.
A data base was developed with information on every polygon (Appendix 9 in Pearsall and Whistler 1991a). This data base includes fields for the map unit; the island; the vegetation map code; the vegetation type; the most common species observed; comments including land-use, general condition, and/or protected status; the occurrence name (assigned on the basis of the nearest geographic feature or village); associated map units (for use when a vegetation occurrence occurs on more than one map); and comments on damage from tropical cyclone Ofa.

3.1.3.3 Unmappable Occurrences

Vegetation sites equal to or smaller than 40 m in any direction were not large enough to map at a scale of 1:20,000. At that scale, 40 m is represented by 2 mm. Map lines are .5 mm wide and are drawn with an estimated margin of error of ±1 millimeter. Two parallel lines drawn to represent a separation of 40 m will converge if they are displaced toward each other by the maximum margin of error.

A few vegetation types were originally described but were not mappable at 1:20,000 and thus could not be included in the final analyses. Most notable of these were Herbaceous Strand Communities and Riparian Woodlands. These are found in narrow patches along ecotones (Herbaceous Strands along the ecotones of littoral and marine communities, and Riparian Woodlands along the ecotones of mesic terrestrial and hydric terrestrial or aquatic communities). Fernland is a patchy, often anthropogenic, edaphic and fire disclimax in the Ridge Rain Forest. Several large
examples of Fernland were mapped on the northern ridges of 'Upolu, but many other occurrences were too small to map. When native vegetation types were not large enough to map at 1:20,000, they were documented in the text describing individual sites (Appendix 9 in Pearsall and Whistler 1991a).

3.1.3.4 Classifying Disturbance

A site was defined as disturbed if swiddens made up some, but less than half, of its area; if selective cutting of vegetation was apparent during field inspection but had affected less than half of the area; if domestic or feral livestock (especially pigs) were significantly present (an influence on vegetation processes); if disclimax patches were maintained by human interference (small swiddens, fernland patches); or if non-native plant species were present but not dominant.

Non-native species were rarely present in the absence of other forms of disturbance. Most mechanical disturbances apparently are followed or accompanied by the introduction of non-native species. Sites dominated by non-native species or where mechanical disturbance was pervasive were not considered as sites for native vegetation types but rather as non-native vegetation types (managed or abandoned

3 Funtumia elastica provided the significant exception. It is a tree with highly mobile, wind-distributed seeds capable of germinating and growing to maturity in dense shade. This species, introduced (in the 1930s?) as a possible crop tree for rubber production, is a very serious threat to Lowland Rain Forests. It is well established as a mono-specific understory in the disturbed Lowland Rain Forests of western 'Upolu.
lands) and were not mapped. Secondary mesic forests large enough to map at 1:20,000 were always disturbed, mainly by the presence of non-native species, as opposed to natural gaps which were rarely large enough to map at this scale, so the "D" code was always included as a prefix to "SM." Secondary shrubland seres following large scale forest disturbances were always dominated by non-native species, and thus were not mapped.

Disturbance Classification and Mapping Summary

I. Native Vegetation types - dominated by native species (mapped)
   A. not disturbed (no D prefix)
   B. disturbed (D prefix) - one or more of:
      1. non-native plant species present but not dominant
      2. clearings, selective cutting on less than half the area
      3. domestic or feral animals significantly present

II. Non-native Vegetation types - dominated by non-native species or mechanical disturbance (not mapped)

3.1.3.5 Incorporation of SPOT Satellite Data

The set of vegetation overlays was, at this point, completed based on air photo interpretation and field verification. The next step was to incorporate SPOT satellite data as a check against and enhancement of the maps.

The Institut français de recherche pour l'exploitation de la mer (IFREMER) working through the Station polynésienne de télédétection in Papeete, Tahiti, French Polynesia (the Station) (Appendix A) provided a radiometrically but non-geometrically
corrected image with less than 10% cloud cover. The data were collected on 1 September 1986 at 21:51:09 UTC. Only the three 20 m resolution bands were used.

The original SPOT image included 3,001 lines of data north to south and 3,190 lines of data east to west (image taken slightly off-nadir). The Station terminal was restricted to 1024 lines of data in each direction, so choices included sampling one ninth of the pixels in the SPOT image (every third line in each direction) or dividing the image into nine sub-images to fit the screen. Since the goal of the image enhancement project was to define the best possible edges around individual vegetation types, the latter course was selected. All experimental procedures were tested on one or more sub-images.

Following the creation of sub-images for enhancement, the next necessary step was to create masks for each sub-image to eliminate interference from variation in reflectance values for the ocean and clouds. One approach was to calculate the Nominal Vegetation Index for each pixel:

\[
NVI = \frac{IR-R}{IR+R}
\]  

(2)

where

NVI is the Nominal Vegetation Index,
IR is the value for infra-red reflectance, and

R is the value for red reflectance.

A study of the NVI image histograms indicated that pixels with very low NVI ($\leq 0.1$) supported virtually no vegetation). These were then set to zero (black) in all bands. The mask was then manually edited along the coast where shallow waters sometimes resulted in higher NVI values (probably due to seagrasses or algae). The final mask was merged with the sub-image to create a new sub-image with all cloud and ocean pixels set to zero. This approach worked very well for masking ocean pixels, but it did not work well for clouds and cloud shadows, masking some but not all pixels. It also sometimes masked recent volcanics and littoral features.

A second approach to masking the sub-images was based on creating three masks, one each for oceans, shadows, and clouds. These masks were based on the presentation values (0-255) of color hue, saturation, and intensity$^4$ on the RGB monitor of the Station computer. Hue was assigned to red, saturation was assigned to blue, and intensity was assigned to green. Since water reflects virtually no infra-red, an oceans mask was created by setting all hue values below 45 (low red value on the screen = low near infra-red reflectance) to zero. Cloud and tree shadows were masked by setting pixels with color intensities below 30 to zero. Clouds were masked

$^4$These characteristics are also referenced as hue, chroma, and value; or hue, saturation, and brightness; and are based on the Munsell Color System as modified by the Optical Society of America (MacAdam 1985, pp. 163-174).
by setting pixels with color saturation below 90 to zero. These masks were merged by minimum values into a single black mask (values = zero) which was then merged by multiplication with the sub-image. The result was nominally better than the NVI masked sub-image, but not worth the additional effort.

Since cloud cover was less than 10%, it was decided to use a mask for ocean pixels only. This mask was created by setting pixels with near infrared below 45 to 255 (maximum) for all three colors, followed by manual editing along coastal areas. This approach was perfectly adequate for ocean masking, and clouds and cloud shadows were rare enough to ignore.

The next step was to enhance contrast in the image as much as possible in order to distinguish terrestrial vegetation types with complex and sometimes very fuzzy edges (wide ecotones). There are usually differences between the same image as presented on the screen and as printed, plotted, or projected by various output devices. This was certainly true in the present case, and since the goal was to produce a paper product for later use with the existing vegetation overlays, all approaches to contrast enhancement were finally evaluated by examination of output from the Station raster plotter.

One set of synthetic variables was created for evaluation. NVI was calculated (Equation 2) and assigned to green on the Station monitor. Brightness was calculated
(Equation 3) and assigned to red on the monitor. Texture was calculated as the standard deviation of the single band reflectance for the central pixel in a moving 3x3 pixel window (Equation 4). In this case, IR was selected as most closely related to vegetation, and the synthetic variable for texture was assigned to blue on the Station monitor. The brightness, vegetation, texture data set was labeled BVT for reference.

\[ B = \sqrt{R^2 + IR^2} \]  \hspace{1cm} (3)

where

B is Brightness,

IR is the value for infra-red reflectance, and

R is the value for red reflectance.

\[ T = s = \sqrt{\frac{\sum_{i=1}^{9} (IR_i - \bar{IR})^2}{9}} \]  \hspace{1cm} (4)

where

T is Texture,
s is the standard deviation, and

IR is the value for infra-red reflectance.

The next step in the process was to bracket the color saturation assignments for red, green, and blue for both the normal and BVT images. Manual experimentation with bracket placement to maximize contrast resulted in the thresholds (range 0-255) shown in Table 3.

<table>
<thead>
<tr>
<th></th>
<th>RED</th>
<th></th>
<th>GREEN</th>
<th></th>
<th>BLUE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>LOW</td>
<td>HIGH</td>
<td>LOW</td>
<td>HIGH</td>
<td>LOW</td>
</tr>
<tr>
<td>NORMAL</td>
<td>65</td>
<td>170</td>
<td>10</td>
<td>20</td>
<td>25</td>
</tr>
<tr>
<td>BVT</td>
<td>30</td>
<td>75</td>
<td>215</td>
<td>245</td>
<td>2</td>
</tr>
</tbody>
</table>

The third step in the process of contrast enhancement was to decide how best to distribute color saturation assignments within the bracketed ranges. Linear and log_{10} distributions for both masked BVT and masked normal data sets (masked) were tested.

A third technique for contrast enhancement is to divide reflectance values (or synthetic variable values) into approximately equally populated classes. The equipopulation algorithm used by the station automatically selects low and high
threshold values by eliminating classes with very few members. Color saturation assignments are then evenly distributed across the equipopulated classes. Equipopulation contrast enhancements were tried for both BVT and original data sets. In these cases, approximately 40 classes were defined in the red band, and less than 20 classes each were generated in the blue and green bands.

Six contrast enhanced images were evaluated according to the ease with which boundaries between forest and non-forest vegetation types could be detected (forest edges); the ease with which different, contiguous forest types could be distinguished, (within-forest edges); and the overall quality of the image as a visual representation of the landscape. Comparisons of the six contrast enhanced sub-images for evaluating vegetation boundaries are summarized in Table 4.

Table 4. Evaluation of Contrast Enhancement Methods

<table>
<thead>
<tr>
<th></th>
<th>FOREST EDGE</th>
<th>WITHIN-FOREST EDGE</th>
<th>OVERALL</th>
</tr>
</thead>
<tbody>
<tr>
<td>NORM., LIN. ENH.</td>
<td>fair</td>
<td>fair</td>
<td>fair</td>
</tr>
<tr>
<td>NORM., LOG\textsubscript{10} ENH.</td>
<td>good</td>
<td>fair</td>
<td>fair</td>
</tr>
<tr>
<td>NORM., EQUIPOP.</td>
<td>good</td>
<td>good</td>
<td>good</td>
</tr>
<tr>
<td>BVT, LIN. ENH.</td>
<td>poor</td>
<td>fair</td>
<td>poor</td>
</tr>
<tr>
<td>BVT, LOG\textsubscript{10} ENH.</td>
<td>poor</td>
<td>fair</td>
<td>poor</td>
</tr>
<tr>
<td>BVT, EQUIPOP.</td>
<td>poor</td>
<td>good</td>
<td>fair</td>
</tr>
</tbody>
</table>
One final experiment was performed to determine if contrast enhancement could be usefully extended by calculating NVI for the masked image and then creating a low density vegetation mask by setting a lower threshold for NVI < .5.

Equipopulation versions of sub-images were prepared with the ocean and low density vegetation masks and the ocean and high density vegetation (inverse of low-density vegetation) masks in place. The two versions required separate evaluation. They could not be concatenated because the same colors represented very different conditions in the two images (e.g., the highest density vegetation in each version is represented by the same colors, but the full range of lower density vegetation in the high density version lay in between them). Forest edge and within-forest edge detection were superior in this last approach, but the overall value of the versions for visualizing the landscape, and the difficulty of overlaying the individual versions with maps, ultimately lead to the rejection of this approach. Linear contrast enhancement of masked normal data subdivided into equipopulated groups finally was chosen for the study.

Because the SPOT image in question had not been geometrically (geographically) rectified, the sub-images could not be directly overlaid with existing maps. Two approaches were tested for basic geographic correction. The first involved digitizing the coastline, roads, and volcanic peaks and then electronically overlaying (on the Station monitor) the digitized plot with the contrast enhanced sub-image. Mutual points were identified, and the entire sub-image was resampled and
geometrically rectified to the digitized plot using an Intergraph geographic information system (the technique is discussed in Jensen 1986, pp. 104-115). The alternative approach involved electronically rotating the sub-image -9° around its center to correct it to true north. The latter approach produced a result that could not be distinguished from the geometrically rectified sub-image, so it was chosen for its ease of application.

Based on the experience discussed in the previous paragraphs, the following process was adopted for sub-image enhancement and printing:

a. Generate an oceans mask by setting near infrared ≤ 45 to zero.

b. Manually edit the mask to correct the coastline.

c. To the unmasked original, apply the transfer function created for equipopulation contrast enhancement.

d. Merge the mask with the equipopulation version of the sub-image.

e. Rotate the image -9° to correct geographically.

f. Print 1:20,000 plots.

This process resulted in nine paper images at 1:20,000 for comparison and incorporation with the existing maps and vegetation overlays for Western Savai’i. These images were overlaid with the existing maps, and draft overlays prepared from aerial photography and field research and corrections were made as follows:
a. Because the SPOT images produced very precise forest-non-forest edge data, coastal and lowland rain forest edges were corrected to the SPOT images, except where field data indicated that timber harvesting probably had reduced the forest area since the SPOT data was collected in 1986. Lava field edges also were corrected to the SPOT images.

b. The ecotones between montane, ridge, and lowland rain forests and cloud forests were adjusted using the SPOT data, since it was superior to the aerial photography.

c. The SPOT images were not as useful as the aerial photographs for visually differentiating coastal wetlands and littoral vegetation types from surrounding land-uses, so these edges were not corrected.

3.1.3.6 Data Confidence

The problem with SPOT data and non-forest edges seems to have been twofold. First, relatively low vegetation density in some non-forest types permitted soil, rock, and water reflectance values to contribute heavily to the vegetation reflectance signatures, resulting in radiometric similarity to other low vegetation density land-uses. Second, most sites for non-forest types are very small, as are patches for most land-uses in the coastal region, so individual vegetation sites tended to be visually lost in areas of high pixel heterogeneity. Fortunately, these were the vegetation types most frequently visited during the field work, and confidence in their mapped positions and boundaries was relatively high.
The SPOT data proved to be very useful for forest type distinction and for forest-non-forest edge definition. SPOT data increased overall confidence levels dramatically, as they provided the very information that was hardest to extract from aerial photographs and to collect in the field.

Lower resolution aerial photography significantly decreased confidence levels, since stereoscopic interpretation (even at 10 power magnification) was very difficult, especially for forest-forest edges. Older aerial photography (1981 versus 1987) resulted in relatively little confidence reduction since changes in forest-non-forest edges usually were caused by recent logging or clearing for agriculture. These changes were relatively easy to find and adjust in the field.

3.1.3.7 Map Data Regions

Following the incorporation of SPOT data, the vegetation overlays for Western Samoa could be divided into "data regions" based on the types of data that were used in their preparation (Figures 5 and 6). Rough confidence levels were estimated for these data regions based on field experience and comparison between data types within region:

Region A  (confidence level high)
1987 aerial photography (1:50,000)
1986 SPOT data (1:20,000)
field work in 1989

Region B  (confidence level moderate)
1987 aerial photography (1:50,000)
field work in 1989
Region C  
(confidence level very high)  
1981 aerial photography (1:20,000)  
1986 SPOT data (1:20,000)  
field work in 1989

Region D  
(confidence level moderate)  
1981 aerial photography (1:20,000)  
field work in 1989

Region E  
(confidence level very high)  
1981 aerial photography (1:20,000)  
field work from 1973 through 1981 (Whistler 1983)

Data region E was a high confidence region in spite of the older photography and the lack of field visits in 1989, because the Aleipata Islands had been extensively visited by Whistler from 1973 - 1981 (Whistler 1983) and are rarely visited by Samoans. Within all data regions except E, lower elevation sites were more easily and therefore more frequently visited than higher elevation sites, and higher elevations were more often obscured by clouds in both SPOT and aerial images. Confidence levels, especially for forest-forest edges, decreased with elevation in data regions A-D.
Figure 5. Savai'i Vegetation Data Confidence Regions
Figure 6. 'Upolu Vegetation Data Confidence Regions
3.1.3.8 The Final Terrestrial Vegetation Maps

The incorporation of these data regions and corrections from SPOT data plus corrections from the post-cyclone reconnaissance in 1990 resulted in the final set of velum overlays produced by the project. A flatbed photocopier was used to make 1:1 velum copies for SPREP, the governments of Western Samoa and New Zealand, IFREMER, the East-West Center, The Nature Conservancy, and the United Nations GRID program in Bangkok (see Appendix 1 for the roles of these agencies). A copy stand was used to make black and white, 4" x 5" panchromatic photographs of each overlay, and archive sets of 4" x 5" negatives were prepared.

3.2 Building a Geographic Information System

3.2.1 Selecting a GIS and Digitizing the Data

The Western Samoa vegetation mapping project originally called for the vegetation data to be digitized and loaded into a fairly simple, grid-based (raster) geographic information system (GIS) such as OSU Map for the PC (Geography Department, Ohio State University) or Idrisi (Graduate School of Geography, Clark University). However, at the same time that the vegetation mapping project was underway, Western Samoa was contracting with ANZDEC Limited and the New Zealand Department of Science and Industrial Research (DSIR), Division of Land and Soil Sciences with funds provided by the Asian Development Bank (ADB) to establish a state-of-the-art natural resources GIS based on Arc-Info (Environmental Systems Research Institute, Inc.) (ANZDEC Ltd. and DSIR Division of Land and Soil
At the urging of ADB and SPREP, negotiations with the ANZDEC/DSIR team were entered, and it was agreed that the vegetation data would be digitized and loaded into the Arc-Info system in Western Samoa, and that a complete copy of the resulting database would be provided for this study and for The Nature Conservancy’s (TNC) proposed Conservation Data Center (see Appendix A).

The ANZDEC/DSIR project was completed some months before the vegetation mapping project. Unfortunately, the Western Samoan Arc-Info GIS fell into disrepair and disuse before either the vegetation data could be entered or the ANZDEC/DSIR data could be extracted and delivered. However, a copy of the ANZDEC/DSIR data had been deposited with the United Nations Environmental Programme Global Resource Information Database (UNEP GRID) office in Bangkok, Thailand. UNEP GRID were building an Arc-Info GIS for the Asia-Pacific region. After complex and lengthy negotiations, the governments of Western Samoa and New Zealand and the managers of ANZDEC and ADB agreed for the UNEP GRID offices to digitize the vegetation data and to release the entire database including the ANZDEC/DSIR data in Arc-Info digital form. In exchange, digital and velum copies of the vegetation data were provided to all of those listed above.

The Arc-Info data required about 30 megabytes of storage, so the next task was to find an Arc-Info system with at least twice and preferably three times that much free disk space for storage, analysis, and modelling. Unfortunately, no such
system existed at the University of Hawaii or the East-West Center, so it was decided to return to the original plan of using a smaller, grid-based system on a personal computer. This would make the process much simpler, at a significant cost in lost resolution. Idrisi was selected, and the process of converting the data to Idrisi format began.

3.2.2 Converting Arc-Info Data to Idrisi Data

A three step process was used to create Arc-Info files that Idrisi could import and convert to Idrisi format:

a. Sub-directory connections in the UNEP GRID data had been corrupted when the data were copied to diskette, so the Arc module EXTERN33 was used to repair these;

b. Arc module @ARC33-34 was used to convert the data from Arc version 3.3 to version 3.4; and

c. Arc module UNGEN was used to create "ungenerated" or line files without topology in a format that Idrisi could read.

The resulting line files were converted to Idrisi vector files using the Idrisi module ARCIDRIS.
3.2.3 Loading the Data

The following parameters were used for the creation of Idrisi image (raster) files on Savai'i and 'Upolu:\(^5\)

<table>
<thead>
<tr>
<th>Table 5. Idrisi File Parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>( Y_{\text{max}} ) (UTM)</td>
</tr>
<tr>
<td>( Y_{\text{min}} ) (UTM)</td>
</tr>
<tr>
<td>( X_{\text{max}} ) (UTM)</td>
</tr>
<tr>
<td>( X_{\text{min}} ) (UTM)</td>
</tr>
<tr>
<td>( Y ) EXTENT</td>
</tr>
<tr>
<td>( X ) EXTENT</td>
</tr>
<tr>
<td>ROWS</td>
</tr>
<tr>
<td>COLUMNS</td>
</tr>
<tr>
<td>CELL SIZE</td>
</tr>
</tbody>
</table>

Using these parameters, vector files were edited for conformity, and image files were created using the following steps:

a. The Idrisi module IMAGE was used to create a blank image file with the correct parameters;

b. The Idrisi module LINERAS was used to write the vector file onto the new image file;

\(^5\) 'Upolu, unless otherwise specified, is understood to include the offshore islands of Apolima, Manono, and the Aleipata Islands.
c. The Idrisi module GROUP was then used to give each resulting polygon a unique number;

d. The resulting unique polygons were manually regrouped and assigned values using paper copies of the original ANZDEC/DSIR maps. This process involved using the IDRISI modules ASSIGN, RECLASS, and UPDATE along with periodic correction using the OVERLAY module along with ocean masks (with non-land cells set to zero); and

e. Individual palette files were created for each data class.

This process resulted in the following data files for both Savai’i and ‘Upolu in the Western Samoa GIS:

Vector files: coasts, roads, and streams (from ANZDEC/DSIR data)

Raster files: vegetation by vegetation type (14 classes), regions of vegetation disturbance and nativity (4 classes), and vegetation data regions (5 regions) (from Pearsall and Whistler); prime agricultural land (1 class), and land tenure (5 classes) (from ANZDEC/DSIR)

In addition to these data files, the geology of Western Samoa was digitized directly into Idrisi from geology maps prepared by the New Zealand Geological
Survey (Kear and Wood 1959)\(^6\), resulting in raster files for sedimentary substrates (3 classes) and volcanic substrates (6 classes). Finally, 500 ft contours were digitized directly from New Zealand Map Series 174 (1976-1988). The 500 ft contour files were converted to 100 m contour vector files by interpolation and reclassification (Idrisi modules INTERCON and RECLASS). The 100 m contours were then variously treated to generate the following additional files:

a. 100 m contours (raster, Idrisi modules INITIAL and LINERAS);

b. digital elevation models with elevations rounded to the nearest meter (raster, Idrisi modules INTERCON and CONVERT); and

c. elevation classes (the first 20 m of elevation, the following 80 m of elevation, and thereafter 100 m intervals, each class identified by its median elevation, e.g., 100-199 m interval identified as the 150 m class) (20 classes on Savai‘i, 13 classes on 'Upolu) (raster, Idrisi modules ASSIGN and RECLASS).

\(^6\)Geology was chosen over soils for the data base for several reasons. The geologic substrates of Western Samoa are relatively young, very well differentiated, and, combined with slope and elevation, closely correspond with soil types (ANZDEC Ltd. and DSIR Division of Land and Soil Sciences 1990; Kear and Wood 1959, 1962; Wright 1962, 1963). The characteristic scale for geologic map units is of the same order of magnitude as the characteristic scale for terrestrial vegetation (see Tables 6, 11, and 12), while the characteristic scale for soil types is one to two orders of magnitude smaller. When tested, the ANZDEC/DSIR soils data set and a digitizing trial on the Wright (1963) maps both produced Idrisi images in which all cells were boundary cells.
Tables 6 - 13 summarize the raster data classes and their descriptive statistics for each of the two main islands. Figures 5-18, following the tables, illustrate the database established in Idrisi on which the modelling and analyses in the following chapters were based.
### Table 6. Native Vegetation Map Units and Areas

<table>
<thead>
<tr>
<th>TYPE NO.</th>
<th>DEFINITION</th>
<th>'UPOLU UNITS</th>
<th>SAVAI'I UNITS</th>
<th>'UPOLU AREA (ha)</th>
<th>SAVAI'I AREA (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Swamp Forest</td>
<td>20</td>
<td>2</td>
<td>967.68</td>
<td>99.00</td>
</tr>
<tr>
<td>2</td>
<td>Herb. Marsh</td>
<td>16</td>
<td>19</td>
<td>314.88</td>
<td>436.50</td>
</tr>
<tr>
<td>3</td>
<td>Mangrove</td>
<td>27</td>
<td>9</td>
<td>1062.40</td>
<td>117.00</td>
</tr>
<tr>
<td>4</td>
<td>Coastal RF</td>
<td>10</td>
<td>9</td>
<td>189.44</td>
<td>895.50</td>
</tr>
<tr>
<td>5</td>
<td>Lowland RF</td>
<td>26</td>
<td>19</td>
<td>17320.96</td>
<td>24878.25</td>
</tr>
<tr>
<td>6</td>
<td>Ridge RF</td>
<td>15</td>
<td>0</td>
<td>6689.28</td>
<td>0</td>
</tr>
<tr>
<td>7</td>
<td>Fernland</td>
<td>14</td>
<td>0</td>
<td>38.40</td>
<td>0</td>
</tr>
<tr>
<td>8</td>
<td>Montane RF</td>
<td>18</td>
<td>3</td>
<td>17059.84</td>
<td>46939.50</td>
</tr>
<tr>
<td>9</td>
<td>Cloud Forest</td>
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<td>1</td>
<td>0</td>
<td>8172.00</td>
</tr>
<tr>
<td>10</td>
<td>Grassland</td>
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<td>0</td>
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</tr>
<tr>
<td>11</td>
<td>Volc. Succ.</td>
<td>0</td>
<td>10</td>
<td>0</td>
<td>9992.25</td>
</tr>
<tr>
<td>12</td>
<td>Litt. Scrub</td>
<td>2</td>
<td>0</td>
<td>148.48</td>
<td>0</td>
</tr>
<tr>
<td>13</td>
<td>Litt. Shrub</td>
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<td>5</td>
<td>56.32</td>
<td>139.50</td>
</tr>
<tr>
<td>14</td>
<td>Litt. Forest</td>
<td>7</td>
<td>11</td>
<td>92.16</td>
<td>821.25</td>
</tr>
<tr>
<td>15</td>
<td>Secondary RF</td>
<td>22</td>
<td>9</td>
<td>3059.20</td>
<td>5697.00</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td></td>
<td><strong>179</strong></td>
<td><strong>98</strong></td>
<td><strong>46999.04</strong></td>
<td><strong>98237.25</strong></td>
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<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>MAX</strong></td>
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<td>27</td>
<td>19</td>
<td>17320.96</td>
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<td><strong>MEAN</strong></td>
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<td>11.93</td>
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<td>3133.27</td>
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<td><strong>STAND. DEV.</strong></td>
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<td>9.68</td>
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<td>5976.94</td>
<td>13037.50</td>
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<td>TYPE NO.</td>
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<td>'UPOLU UNITS</td>
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<td>'UPOLU AREA (ha)</td>
<td>SAVAI'I AREA (ha)</td>
</tr>
<tr>
<td>---------</td>
<td>--------------------</td>
<td>--------------</td>
<td>---------------</td>
<td>------------------</td>
<td>-------------------</td>
</tr>
<tr>
<td>1</td>
<td>Native</td>
<td>55</td>
<td>20</td>
<td>31091.20</td>
<td>88236.00</td>
</tr>
<tr>
<td>2</td>
<td>Dist. Native</td>
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<td>28</td>
<td>12792.32</td>
<td>4304.25</td>
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<tr>
<td>3</td>
<td>Secondary (dist.)</td>
<td>19</td>
<td>9</td>
<td>3059.20</td>
<td>5697.00</td>
</tr>
<tr>
<td>4</td>
<td>Non-native</td>
<td>48</td>
<td>84</td>
<td>68789.76</td>
<td>74126.25</td>
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</table>

TOTAL: 179 141 | 115732.48 | 172363.50

MIN: 19 9 | 3059.20 | 5697.00

MAX: 57 84 | 68789.76 | 88236.00

MEAN: 44.75 35.25 | 28933.12 | 43090.88

STAND. DEV.: 17.95 33.42 | 29001.12 | 44362.07
Table 8. Vegetation Data Confidence Regions

<table>
<thead>
<tr>
<th>TYPE NO.</th>
<th>DEFINITION</th>
<th>'UPOLU UNITS</th>
<th>SAVAI'I UNITS</th>
<th>'UPOLU AREA (ha)</th>
<th>SAVAI'I AREA (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>A. High</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>118815.75</td>
</tr>
<tr>
<td>2</td>
<td>B. Moderate</td>
<td>1</td>
<td>2</td>
<td>60221.44</td>
<td>32449.50</td>
</tr>
<tr>
<td>3</td>
<td>C. Very high</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>3258.00</td>
</tr>
<tr>
<td>4</td>
<td>D. Moderate</td>
<td>1</td>
<td>1</td>
<td>55265.28</td>
<td>17858.25</td>
</tr>
<tr>
<td>5</td>
<td>E. Very high</td>
<td>1</td>
<td>0</td>
<td>271.36</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>TOTAL</td>
<td>3</td>
<td>5</td>
<td>115758.08</td>
<td>172381.50</td>
</tr>
</tbody>
</table>

MIN: 0 0 271.36 3258.00
MAX: 1 2 60221.44 118815.75
MEAN: 0.60 1.00 23151.62 34476.30
STAND. DEV.: 0.56 0.77 31626.57 48878.95

Table 9. Primary Agricultural Land*

<table>
<thead>
<tr>
<th>TYPE NO.</th>
<th>DEFINITION</th>
<th>'UPOLU UNITS</th>
<th>SAVAI'I UNITS</th>
<th>'UPOLU AREA (ha)</th>
<th>SAVAI'I AREA (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Prime Ag Land</td>
<td>133</td>
<td>41</td>
<td>21548.12</td>
<td>17174.25</td>
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</tbody>
</table>

*Primary Agricultural Land is "Class 1 Land with few limitations to agricultural use" as described by ANZDEC and DSIR (1990, p. 83).
Table 10. Land Tenure Classes

<table>
<thead>
<tr>
<th>TYPE NO.</th>
<th>DEFINITION</th>
<th>'UPOLU UNITS</th>
<th>SAVAI'I UNITS</th>
<th>'UPOLU AREA (ha)</th>
<th>SAVAI'I AREA (ha)</th>
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</thead>
<tbody>
<tr>
<td>1</td>
<td>Customary</td>
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<td>2</td>
<td>70072.32</td>
<td>148317.75</td>
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<tr>
<td>2</td>
<td>Leased*</td>
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<td>4</td>
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<td>5553.00</td>
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<tr>
<td>3</td>
<td>Freehold</td>
<td>28</td>
<td>7</td>
<td>11430.40</td>
<td>1140.75</td>
</tr>
<tr>
<td>4</td>
<td>WSTEC</td>
<td>23</td>
<td>5</td>
<td>9213.44</td>
<td>4605.75</td>
</tr>
<tr>
<td>5</td>
<td>Government</td>
<td>22</td>
<td>11</td>
<td>19850.24</td>
<td>12449.25</td>
</tr>
<tr>
<td></td>
<td>TOTAL</td>
<td>88</td>
<td>29</td>
<td>113697.28</td>
<td>172066.50</td>
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<td>1</td>
<td>2</td>
<td>9213.44</td>
<td>1140.75</td>
</tr>
<tr>
<td></td>
<td>MAX</td>
<td>28</td>
<td>11</td>
<td>70072.32</td>
<td>148317.75</td>
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<tr>
<td></td>
<td>MEAN</td>
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<td>5.80</td>
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<td>34413.30</td>
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<td>STAND. DEV.</td>
<td>10.55</td>
<td>3.42</td>
<td>27129.74</td>
<td>63806.57</td>
</tr>
</tbody>
</table>

*Leased land is customary land that is leased mainly by the government or by WSTEC.
Table 11. Sedimentary Substrates

<table>
<thead>
<tr>
<th>TYPE NO.</th>
<th>DEFINITION</th>
<th>'UPOLU UNITS</th>
<th>SAVAI'I UNITS</th>
<th>'UPOLU AREA (ha)</th>
<th>SAVAI'I AREA (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Swamp Alluvium</td>
<td>39</td>
<td>4</td>
<td>1856.00</td>
<td>974.25</td>
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<tr>
<td>2</td>
<td>Coastal Alluvium</td>
<td>73</td>
<td>17</td>
<td>3793.92</td>
<td>1631.25</td>
</tr>
<tr>
<td>3</td>
<td>Vini Tuff*</td>
<td>6</td>
<td>0</td>
<td>335.36</td>
<td>0</td>
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<tr>
<td></td>
<td><strong>TOTAL</strong></td>
<td><strong>118</strong></td>
<td><strong>21</strong></td>
<td><strong>5985.28</strong></td>
<td><strong>2605.5</strong></td>
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<tr>
<td></td>
<td><strong>MIN</strong></td>
<td><strong>6</strong></td>
<td><strong>0</strong></td>
<td><strong>335.36</strong></td>
<td><strong>0</strong></td>
</tr>
<tr>
<td></td>
<td><strong>MAX</strong></td>
<td><strong>73</strong></td>
<td><strong>7</strong></td>
<td><strong>3793.92</strong></td>
<td><strong>1631.25</strong></td>
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<tr>
<td></td>
<td><strong>MEAN</strong></td>
<td><strong>33.50</strong></td>
<td><strong>8.89</strong></td>
<td><strong>1995.09</strong></td>
<td><strong>868.50</strong></td>
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<tr>
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<td><strong>STAND. DEV.</strong></td>
<td><strong>27.60</strong></td>
<td><strong>6.80</strong></td>
<td><strong>1733.47</strong></td>
<td><strong>820.75</strong></td>
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</table>

*Apolima and the Aleipata Islands; last inter-glacial (Kear and Woods 1959)
Table 12. Volcanic Substrates

<table>
<thead>
<tr>
<th>TYPE NO.</th>
<th>DEFINITION</th>
<th>'UPOLU UNITS</th>
<th>SAVAI'I UNITS</th>
<th>'UPOLU AREA (ha)</th>
<th>SAVAI'I AREA (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Aopo Volcanics (youngest, historic, little weathered)</td>
<td>0</td>
<td>14</td>
<td>0</td>
<td>12449.25</td>
</tr>
<tr>
<td>2</td>
<td>Puapua Volcanics (Middle to late Holocene)</td>
<td>98</td>
<td>51</td>
<td>3182.08</td>
<td>47074.50</td>
</tr>
<tr>
<td>3</td>
<td>Lefaga Volcanics (early Holocene)</td>
<td>7</td>
<td>0</td>
<td>12902.40</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>Mulifanua Volcanics (last glaciation)</td>
<td>25</td>
<td>151</td>
<td>25518.08</td>
<td>65504.25</td>
</tr>
<tr>
<td>5</td>
<td>Salani Volcanics (penultimate glaciation and last inter-glacial period, late Pleistocene)</td>
<td>47</td>
<td>71</td>
<td>45478.40</td>
<td>42102.00</td>
</tr>
<tr>
<td>6</td>
<td>Fagaloa Volcanics (oldest, Pliocene to mid-Pleistocene, includes talus slopes, extremely weathered and eroded) (Kear and Wood 1959)</td>
<td>49</td>
<td>11</td>
<td>22666.24</td>
<td>2603.25</td>
</tr>
<tr>
<td>TOTAL</td>
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* Aopo Volcanics (youngest, historic, little weathered), Puapua Volcanics (Middle to late Holocene), Lefaga Volcanics (early Holocene), Mulifanua Volcanics (last glaciation), Salani Volcanics (penultimate glaciation and last inter-glacial period, late Pleistocene), Fagaloa Volcanics (oldest, Pliocene to mid-Pleistocene, includes talus slopes, extremely weathered and eroded) (Kear and Wood 1959).
Table 13. Elevation Classes (median values)

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<th>SAVAI'I UNITS</th>
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<th>SAVAI'I AREA (ha)</th>
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Table 13 (continued). Elevation Classes (median values)

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<th>TYPE NO.</th>
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<th>SAVAI'I UNITS</th>
<th>'UPOLU AREA (ha)</th>
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Figure 7. Savai'i Native Vegetation from Remotely Sensed Data and Field Reconnaissance

SF = Swamp Forest  FL = Fernland
HM = Herbaceous Marsh  CF = Cloud Forest
MG = Mangrove  GL = Grassland
CR = Coastal Rain Forest  VS = Volc. Success.
LR = Lowland Rain Forest  LP = Littoral Scrub
RR = Ridge Rain Forest  LS = Littoral Shrub
MR = Montane Rain Forest  LF = Littoral Forest
SM = Secondary Mesic Forest
blank = non-native vegetation

160
Figure 8. 'Upolu Native Vegetation from Remotely Sensed Data and Field Reconnaissance

SF = Swamp Forest  FL = Fernland
HM = Herbaceous Marsh  CF = Cloud Forest
MG = Mangrove  GL = Grassland
CR = Coastal Rain Forest  VS = Volc. Success.
LR = Lowland Rain Forest  LP = Littoral Scrub
RR = Ridge Rain Forest  LS = Littoral Shrub
MR = Montane Rain Forest  LF = Littoral Forest
SM = Secondary Mesic Forest
blank = non-native vegetation
Figure 9. Savai'i Vegetation Nativity and Disturbance
Figure 10. 'Upolu Vegetation Nativity and Disturbance
Figure 11. Savai'i Prime Agricultural Land
Figure 12. 'Upolu Prime Agricultural Land
Figure 13. Savai'i Land Tenure
Figure 14. 'Upolu Land Tenure
Figure 15. Savai'i Substrates
Figure 16. Upolu Substrates
Figure 17. Savai'i Elevations
Contour Interval = 100 m
Figure 18. 'Upolu Elevations
Contour Interval = 100 m
CHAPTER 4
DEFINING ECOTOPES
AND SETTING PRIORITIES FOR THEIR CONSERVATION

4.1 Defining Ecosystems

Ecosystems are comprised of living organisms and their environments functioning as systems and bounded by the phenomenon of probable interaction. In other words, interactions among ecosystem members and the ecosystem environment are more common than interactions between ecosystem members and external organisms or the external environment. An ecosystem is, in effect, a clustering of more probable interactions in a universe of possible interactions.

4.1.1 The Role of the Topo-edaphic Substrate

The nature of the substrate plays a critical role in determining the nature of the ecosystem, as ecologists, soil scientists, and geologists have long observed (e.g., Alverson 1990, Egler 1959, Trudgill 1977). The shape of the land itself (the landform) plays a significant role in the shaping of ecosystem internal and external interactions (Swanson 1980, Swanson et al. 1988). In a region where moisture is plentiful and temperature fluctuates relatively little, that is, where seasonal climate plays a relatively small role, ecosystems are even more strongly influenced by their substrate. On the other hand, disturbances (e.g., tropical cyclones, fires) and the ability of vegetation to propagate into new areas following disturbance result in
ecosystem boundaries (ecotones) that do not correspond exactly to topo-edaphic substrate boundaries (Wiens et al. 1985).

Based on these assumptions, a suite of ecosystems (ecotopes) was defined for the landscapes of Savai‘i and 'Upolu using vegetation, topographic data, and substrate as the defining parameters. The task was accomplished using Idrisi, and the following summarizes the process:

a. Idrisi module SURFACE was used to create slope and aspect files.

b. Idrisi module RECLASS was used to create aspect classes:
   1) NE, 1°-90°, median value 45°
   2) SE, 91°-180°, median value 135°
   3) SW, 181°-270°, median value 225°
   4) NW, 271°-360°, median value 315°

c. Idrisi module RECLASS was used to create slope classes:
   1) 0°-2°
   2) 3°-6°
   3) 7°-15°
   4) 16°+

d. Idrisi module FILTER: MODE was used as a low-pass or smoothing filter with one pass for aspect and two passes for slope.
e. Idrisi module CROSSTAB was used to cross-tabulate slope and aspect files. This resulted in 16 unique classes.

f. Idrisi module CROSSTAB was used to cross-tabulate elevation and slope-aspect files. This resulted in 320 unique topographic classes.

g. Idrisi module CROSSTAB was used to cross-tabulate topography and geology files. CLUSTER was used to group closely associated landtypes and to eliminate empty or very sparsely populated classes. HISTO and CROSSTAB tables and RECLASS were used to manually check and sometimes modify the new classes. This process resulted in 37 unique landtypes or landform association classes for Savai'i and 50 unique landtypes for 'Upolu. During this process, topography was simplified substantially, resulting in only three general elevation classes:

1) coastal (0-20 m)
2) lowland (21-500 m)
3) montane (501+ m)

and three general slope classes:

1) gentle (0° - 6°)
2) moderate (7° - 15°)
3) steep (16°+).

---

1Note that lowland and montane elevation classes correspond only loosely with lowland and montane vegetation classes.
Aspect was dropped altogether, since it was generally redundant with geologic classes.

h. Finally, vegetation was cross-tabulated with landtypes to generate 87 unique ecotope types for Savai'i and 128 unique ecotope types for 'Upolu.

Figures 19 and 20 illustrate the landtypes of Savai'i and 'Upolu. In these illustrations, red varies directly with substrate age (older substrates are redder), green varies inversely with elevation (lower elevation landtypes are greener), and blue varies directly with slope (steeper landtypes are bluer).
Red varies directly with substrate age (older substrates are redder). Green varies inversely with elevation (lower elevation landtypes are greener). Blue varies directly with slope (steeper landtypes are bluer).
Red varies directly with substrate age (older substrates are redder). Green varies inversely with elevation (lower elevation landtypes are greener). Blue varies directly with slope (steeper landtypes are bluer).
4.1.2 Testing the Correlations Between Vegetation and Landtypes

The Chi Square test\(^2\) was selected to test the null hypothesis that vegetation and landtypes were not significantly correlated. The observed relative frequencies for both vegetation and landtypes were multiplied together to generate expected distributions of vegetation and landtype correlations. These were then used along with observed correlations in the familiar chi square equation (Clark and Hosking 1986, pp. 262-265):

\[
X^2 = \sum_{i=1}^{N} \frac{(O_i - E_i)^2}{E_i} \tag{5}
\]

where

- \(O\) is observed correlations,
- \(E\) is expected (random) correlations, and
- \(N\) is the number of possible correlations.

For Savaiʻi, \(X^2\) was 41206.82 with 468 degrees of freedom, yielding a probability in excess of .999 that the null hypothesis was false and that vegetation and landtypes were positively correlated. For 'Upolu, \(X^2\) was 19525.50 with 507 degrees of freedom, also yielding a probability in excess of .999.

\(^2\)The Chi Square test is appropriate for testing correlations between nominal, non-parametric data sets without zero values. These data met these requirements.
4.1.3 Developing Probable Relationships Between Vegetation and Landtypes

In order to set conservation priorities among ecotopes, it is essential to know which ones are rare and why they are rare. Some will be rare because they have been over-exploited, and some will be rare because their substrate or micro-climate is rare; that is, they are naturally rare. Determining the difference in Western Samoa was complicated by the fact that there was a many-to-many correspondence between landtypes and vegetation types. It was necessary to determine the probability of a given landtype supporting a given vegetation type, including the probability of a given natural ecotope in a given place where no natural ecotope(s) currently occurred.

The technique chosen for this task was Bayesian inference. The Bayes statistic was developed as a method for incrementally increasing the probability of a given hypothesis through testing and/or experience (experiment) (Press 1989, pp. 3-20; Rosenkrantz 1977). The essential content of the theorem is that prior probabilities can be tested, and the results used to develop a new, more accurate set of posterior probabilities. Although the theorem is easily proven (most texts simply state that the proof is "trivial" given the fundamental laws of probability, e.g., Phillips 1974), it is not widely accepted except in its empirical form in which observed data (e.g., relative

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3Bayesian inference is not popular among those who subscribe exclusively to the Popperian doctrine of falsification: In a sufficiently large and varied universe, all hypotheses have no (zero) probability of being true. Inference may only proceed by struggling to falsify (disprove) hypotheses. Successive failures to disprove a hypothesis result in its "corroboration" but do not in any way increase its probability of being true. This is a fundamental tenet of the logical positivism of the Vienna Circle (Hill 1981, Howsen and Urbach 1989, May 1981, Rosenkrantz 1977).
frequencies) are used as the prior probabilities (Robbins 1955). Empirical Bayesian inference is now often employed as a useful technique in remote sensing (e.g., Pereira and Itami 1991, Strahler 1980) and in ecological studies (e.g., Reckhow 1990). This technique was used in this research, following the methodology of Phillips (1974, pp. 56-89) and Reckhow (1990).

A Bayesian statement of the problem was developed. The probability of a given vegetation (hypothetical outcome) occurring for a given landtype (datum) could be stated as:

\[
P(V_{i}|LT_{1}) = \frac{P(V_{i})P(LT_{1}|V_{i})}{\sum_{i=1}^{N} P(V_{i})P(LT_{1}|V_{i})}
\]

where

- \(V_{i}\) is the given vegetation type (hypothesis) for which the probability of co-occurrence with \(LT_{1}\) is sought,
- \(LT_{1}\) is the given landtype (datum),
- \(P(V_{i})\) is the observed relative frequency (prior probability) of vegetation type \(i\),
- \(P(LT_{1}|V_{i})\) is the observed probability (relative frequency or, in Bayesian
terms, likelihood) of \( LT_1 \) occurring given each member of the range of possible vegetation types (\( V_j \)), and

\[ P(V_j|LT_1) \] is the calculated (posterior) probability of \( V_j \) given \( LT_1 \).

The results of applying empirical Bayesian inference to the problem at hand are presented in the following tables. The first four columns summarize the landtypes. In the last column, the ecotope numbers are given followed in parentheses by the vegetation type and its probability of occurrence on that landtype. Missing ecotope numbers are either an artifact of the cross-tabulation process, representing landtype correspondences with non-native vegetation (zero values), or they represent ecotopes with vanishingly small probabilities (less than one half of one percent) that were probably the result of digitizing errors (e.g., tiny overlaps of adjacent polygons or "slivers"). In either case, the missing numbers can be ignored. Landtypes with no native vegetation (indicated as "unknown" in the last column) represent one or more locally extinct ecotope (and possibly vegetation) types.
Table 14. Savai'i Landtypes and Vegetation

| LAND-  | ELEV.  | SLOPE  | GEOLOGIC  | ECOTOPE NO.  |
| TYPE  | CLASS  | CLASS  | SUBSTRATE | (PROB. VEG.) |
| NUMBER |        |        |           |              |
| 1      | Coastal| Gentle | Swamp Alluvium | unknown (SF?) |
| 2      | Lowland| Gentle | Swamp Alluvium | 4 (SF 1.00) |
| 3      | Montane| Gentle | Swamp Alluvium | 5 (SF 1.00) |
| 4      | Montane| Moderate| Swamp Alluvium | 6 (MR 1.00) |
| 5      | Montane| Steep  | Swamp Alluvium | 7 (MR 1.00) |
| 6      | Coastal| Gentle | Coastal Alluvium | 9 (SF 0.18) |
|        |        |        |            | 10 (HM 0.50) |
|        |        |        |            | 11 (MG 0.20) |
|        |        |        |            | 12 (CR 0.06) |
|        |        |        |            | 13 (LS 0.06) |
| 7      | Lowland| Gentle | Coastal Alluvium | 15 (HM 0.49) |
|        |        |        |            | 16 (MG 0.02) |
|        |        |        |            | 17 (CR 0.42) |
|        |        |        |            | 18 (LR 0.07) |
| 8      | Lowland| Moderate| Coastal Alluvium | unknown (CR? LR?) |
| 9      | Coastal| Gentle | Aopo       | 22 (VS 0.90) |
|        |        |        |            | 23 (LS 0.07) |
|        |        |        |            | 24 (LF 0.03) |
| 10     | Lowland| Gentle | Aopo       | 28 (VS 1.00) |
| 11     | Montane| Gentle | Aopo       | 30 (MR 0.54) |
|        |        |        |            | 31 (VS 0.46) |
| 12     | Lowland| Moderate| Aopo      | 33 (VS 1.00) |
| 13     | Montane| Moderate| Aopo     | 35 (MR 0.71) |
|        |        |        |            | 36 (VS 0.29) |
Table 14 (continued). Savai'i Landtypes and Vegetation

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<th>SLOPE CLASS</th>
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Table 14 (continued). Savai’i Landtypes and Vegetation

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<td>210 (LR 0.08) 211 (RR 0.07) 212 (MR 0.85)</td>
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</tbody>
</table>
4.1.4 Spatial Autocorrelation

At this point a correlation set had been developed for future use in the modelling process. Ecotopes were defined as phenomena of probable spatial correlations among a particular set of landtypes and a particular set of vegetation types. Such spatial correlations sometimes appear to be more significant than they actually are due to spatial autocorrelation.

Spatial autocorrelation is the phenomenon that some geographic data tend to be more spatially correlated than can be explained by all external variables. This is generally seen as a statistical problem for geographers, especially those using regression analysis to establish correlations (Haining 1989, Mark 1984, Mark and Church 1977, Mark and Peuker 1978). However, some see this phenomenon more as a missing variable, or as a piece of useful information (e.g., Miron 1984). All of the individual data sets examined so far in this work had spatial autocorrelation indices (Moran's I) in excess of 0.85 (on a scale of 0 to 1.0) using a one lag (out to the first aureole of cells), king's case (including diagonally adjacent cells) test (Idrisi module AUTOCORR). The final ecotope data sets for Savai'i and 'Upolu each had Moran’s I values of 0.88. Both are highly autocorrelated.

Spatial autocorrelation is not an empty statistic. It provides, as Miron (1984) has observed, an avenue to further explanation in data analysis. In the case of vegetation, it is probably a measurement of the degree to which vegetation propagates
itself. For example, following a significant disturbance that eliminates a number of vegetation sites, one would expect to find Lowland Rain Forest reestablishing itself more readily near surviving stands of Lowland Rain Forest that would serve as sources of propagules, pollinators, etc. This is especially true for inland forests that do not include species that are normally invasive or capable of wide dispersal (e.g., rain forests, as contrasted with strand vegetation or volcanic successional species). This tendency operates somewhat independently of any substrate variables. The extent to which it does operate independently can be estimated by an index of spatial autocorrelation. It is very likely that the intrusions of vegetation types onto substrates more closely correlated with other vegetation types is a result of this phenomenon of self-propagation. Spatial autocorrelation indices may be measures of the fuzziness of ecotones in a dynamic landscape of shifting boundaries.

A clear understanding of spatial autocorrelation would thus be essential for making useful predictions of future vegetation patterns based on present patterns. Since the task in the present research was instead to describe the missing vegetation

---

4 The tendency itself is entirely substrate-independent, but the surviving stands of the vegetation type would presumably be wholly or partially correlated with substrate type, so the effect could only be partially independent of substrate.

5 For example, a cost/distance model for vegetation propagation and spread could be developed using an interpolated (multi-lag) spatial autocorrelation index as the inverse of cost (combined with topographic variables, including watershed and windshed boundaries). This could develop into a very useful method for mapping future potential vegetation, a concept that did not emerge in the literature review for this work. It would make an interesting research problem, but it is outside the present scope.
based on present patterns, high measures of spatial autocorrelation provided neither any reason to be suspicious of, nor any useful data for, the developing models. In fact, high spatial autocorrelation reinforces the modelling process because of the phenomenon of self-propagation.

4.2 Mapping the Normative Vegetation of Western Samoa

Many terms are used to describe the vegetation that might be in a place. These include "potential natural vegetation" (Küchler 1964, 1988), "climax vegetation" (Clements 1936, Pfister and Arno 1980, Whittaker 1953) and "pre-settlement vegetation" (Noss 1985). Each has problems. Potential natural vegetation implies that, if human interference were withdrawn, the vegetation would succeed to its identified potential. This concept ignores the effects humans have already had on the substrate and on the species components of vegetation, via introductions and extinctions. It also ignores the potential changes that might be wrought in the species pool and in the substrate by future events. The climax vegetation concept has the same problem, exacerbated by the false notion that vegetation has a climax at which an equilibrium of species composition and distribution will exist. This concept certainly has no validity on islands, where introductions and extinctions are routine, and where tropical cyclones, volcanoes, and tsunami periodically disturb the landscape. The pre-settlement vegetation concept has intellectual validity, but is rendered irrelevant by the passage of time and the very forces of change listed above.
For these reasons, "normative vegetation" was chosen as a new term to identify the probable native-species-dominated vegetation that would exist in a place at this time, given the current pool of native species, and given that humans had not removed and maintained the absence of unmanaged vegetation. There is no assumption that humans could withdraw and normative vegetation would appear. There is no assumption that normative vegetation would be at equilibrium, and there is no assumption that normative vegetation existed at any time in the past. The concept of normative vegetation essentially equilibrates those portions of the landscape not occupied by native-species-dominated vegetation with those portions that are. The landtype combined with the normative vegetation identifies the normative ecotope.

Normative vegetation (and thus, ecotopes) can be divided into two classes: the actual, where normative vegetation exists at this time (by definition) and the nominal, where normative vegetation is only an estimate of a place’s potential. The maps of native vegetation (Figures 7 and 8) are maps of actual vegetation. In statistical terms, the maps of actual vegetation are the sample from which the normative vegetation (the population, even though it is hypothetical) can be estimated and mapped.

The following outline clarifies the relationship among the normative, actual, nominal, and non-normative vegetation types:
I. Normative (hypothetical) Distribution
   A. Actual Occurrences
      1. Primary Occurrences (native vegetation that occupies a place where humans have never removed the majority of the native vegetation cover)
      2. Disturbed Primary Occurrences
      3. Secondary Occurrences (native vegetation that occupies a place where humans have removed the majority of the native vegetation cover)
   B. Nominal Occurrences (non-occurrences; a non-native vegetation type within the normative distribution of a native vegetation type)

II. Non-normative (outside the hypothetical) Distribution

The probabilities in Tables 14 and 15 permit the mapping of normative vegetation and ecotopes. In order to prevent this mapping process from reducing the information content of the GIS, normative vegetation and ecotopes were mapped (Idrisi module ASSIGN), and then actual vegetation and ecotopes were overlaid as a corrective measure (Idrisi module OVERLAY). The maps were prepared as multiple overlays in order to distinguish between measured and predicted vegetation. The first layer shows actual vegetation (Figures 7 and 8), the second layer shows vegetation based on probabilities of 0.75 or more (Figures 21 and 22), and the third (and on 'Upolu, the fourth) layer(s) show the two most probable vegetation types in cases where the probability of neither reaches 0.75 (Figures 23, 24, and 25). When vegetation was entirely unknown, the map unit was assigned a value of zero, indicating an ecotope type that is locally extirpated. Figures 26 and 27 illustrate the normative vegetation maps of Savai’i and 'Upolu.
Figure 21. Savai'i Nominal Vegetation with Probabilities of 75% or More

SF = Swamp Forest
HM = Herbaceous Marsh
MG = Mangrove
CR = Coastal Rain Forest
LR = Lowland Rain Forest
RR = Ridge Rain Forest
MR = Montane Rain Forest
FL = Fernland
CF = Cloud Forest
GL = Grassland
VS = Volc. Success.
LP = Littoral Scrub
LS = Littoral Shrub
LF = Littoral Forest
Figure 22. 'Upolu Nominal Vegetation with Probabilities of 75% or More

SF = Swamp Forest  FL = Fernland
HM = Herbaceous Marsh  CF = Cloud Forest
MG = Mangrove  GL = Grassland
CR = Coastal Rain Forest  VS = Vole. Success.
LR = Lowland Rain Forest  LP = Littoral Scrub
RR = Ridge Rain Forest  LS = Littoral Shrub
MR = Montane Rain Forest  LF = Littoral Forest
Figure 23. Sava\'i Nominal Vegetation with Probabilities Less than 75%
Two Most Likely Candidates

- SF = Swamp Forest
- HM = Herbaceous Marsh
- MG = Mangrove
- CR = Coastal Rain Forest
- LR = Lowland Rain Forest
- RR = Ridge Rain Forest
- MR = Montane Rain Forest
- FL = Fernland
- CF = Cloud Forest
- GL = Grassland
- VS = Volc. Success.
- LP = Littoral Scrub
- LS = Littoral Shrub
- LF = Littoral Forest
Figure 24. "Upolu Nominal Vegetation with Probabilities Less than 75% Two Most Likely Candidates

SF = Swamp Forest
HM = Herbaceous Marsh
MG = Mangrove
CR = Coastal Rain Forest
LR = Lowland Rain Forest
RR = Ridge Rain Forest
MR = Montane Rain Forest
FL = Fernland
CF = Cloud Forest
GL = Grassland
VS = Vole. Success.
LP = Littoral Scrub
LS = Littoral Shrub
LF = Littoral Forest
Figure 25. 'Upolu Nominal Vegetation with Probabilities Less than 75%
Two Most Likely Candidates (continued)

SF = Swamp Forest
HM = Herbaceous Marsh
MG = Mangrove
CR = Coastal Rain Forest
LR = Lowland Rain Forest
RR = Ridge Rain Forest
MR = Montane Rain Forest

FL = Fernland
CF = Cloud Forest
GL = Grassland
VS = Volc. Success.
LP = Littoral Scrub
LS = Littoral Shrub
LF = Littoral Forest
Figure 26. Savai'i Normative Vegetation

SF = Swamp Forest
HM = Herbaceous Marsh
MG = Mangrove
CR = Coastal Rain Forest
LR = Lowland Rain Forest
RR = Ridge Rain Forest
MR = Montane Rain Forest
FL = Fernland
CF = Cloud Forest
GL = Grassland
VS = Volc. Success.
LP = Littoral Scrub
LS = Littoral Shrub
LF = Littoral Forest
Figure 27. 'Upolu Normative Vegetation

SF = Swamp Forest
HM = Herbaceous Marsh
MG = Mangrove
CR = Coastal Rain Forest
LR = Lowland Rain Forest
RR = Ridge Rain Forest
MR = Montane Rain Forest
FL = Fernland
CF = Cloud Forest
GL = Grassland
VS = Volc. Success.
LP = Littoral Scrub
LS = Littoral Shrub
LF = Littoral Forest
There is a problem with the mapping of nominal vegetation. Along the coast and in the uplands, vegetation types exist that are rarely the most probable vegetation type for a given landtype. These include grasslands, swamp forests in cinder cones, and even cloud forest in parts of the uplands. One or more missing variables (perhaps drainage) may account for these anomalies. There are also extirpated ecotopes (and perhaps vegetation types) about which we know nothing, and which we cannot predict retroactively. In the uplands of Savai’i, the problem is minor, because those ecotopes are all still there. Elsewhere in Western Samoa, the problem is serious. The distribution of littoral ecotopes cannot be predicted accurately without knowing whether historically certain littoral types were disturbed or extirpated disproportionately (especially true for Herbaceous Marshes which, as Samoa’s best land for growing taro, were probably disturbed or extirpated more quickly than any other type following Polynesian colonization). Even so, maps of probable normative vegetation are superior to no maps at all, and the indices of depletion, natural rarity, and conservation priority that follow are based on just such data. Fortunately, the confidence level for each nominal polygon can be determined directly from Tables 14 and 15.

4.3 Estimating Depletion of Ecotopes

With the normative vegetation and the landtypes (together comprising the normative ecotopes) of Western Samoa mapped, it was relatively easy to determine the level of depletion of actual ecotopes.
The level of depletion of an ecotope type can be estimated based on spatial measures of relative nativity and disturbance:

\[ P_i = 0.33D_i + 0.67S_i + N_i \]  

(7)

where

- \( P_i \) is the index of Depletion of an ecotope,
- \( D_i \) is the proportion of the ecotope type's normative area that is disturbed primary growth (one third weight),
- \( S_i \) is the proportion of the ecotope type's normative area that is secondary growth (two thirds weight), and
- \( N_i \) is the proportion of the ecotope type's normative area in non-native vegetation (full weight);

so that

\[ 1 - (D_i + S_i + N_i) \] is the proportion of the ecotope type's normative area that is undisturbed primary growth.

Note that the weights assigned to the three variables are easily justifiable in terms of their relative positions. Complete displacement of an ecotope is more radical than simple disturbance, and temporary displacement followed by succession is somewhere in between. However, the assignment of weights at the one third, two thirds, and whole positions is essentially arbitrary (note however that changing the relative weights of the variables will not change the relative ranking of the ecotope
types). An argument could be made effectively that, given the rarity of secondary forests in Western Samoa, and given the suite of non-native species that are incorporated in these forests, secondary growth types should be given much closer to full weight. This is a testable issue, given serial (time series) analyses of the ecotopes of Western Samoa. The strategy here was to provide an equal divisions background on which future workers can improve.

Thirteen (15%) of Savai‘i’s ecotope types have depletion indices in excess of 0.5000, while 52 (60%) had depletion indices of 0.000 indicating no depletion (100% of all locations in primary, undisturbed condition). On 'Upolu, 31 (25%) ecotope types have depletion indices in excess of 0.5000, and only 40 (31%) had depletion indices of 0.000. Savai‘i’s most depleted ecotope is Lowland Rain Forest on lowland, gently sloping Mulifanua substrates. On 'Upolu, the most depleted ecotope is Ridge Rain Forest on coastal, gently sloping Fagaloa substrates. On both islands, the least depleted ecotopes tended to be rare ecotopes at high elevations. Tables 16 and 17 provide lists of the depleted ecotopes on Savai‘i and 'Upolu with indices over 0.5000 (see Tables 14 and 15 for Ecotope descriptions).
Table 16. Depleted Ecotopes of Savai‘i

<table>
<thead>
<tr>
<th>ECOTOPE NUMBER</th>
<th>INDEX OF DEPLETION</th>
<th>ECOTOPE NUMBER</th>
<th>INDEX OF DEPLETION</th>
</tr>
</thead>
<tbody>
<tr>
<td>74</td>
<td>0.9165</td>
<td>124</td>
<td>0.7257</td>
</tr>
<tr>
<td>60</td>
<td>0.9027</td>
<td>48</td>
<td>0.7168</td>
</tr>
<tr>
<td>10</td>
<td>0.9008</td>
<td>33</td>
<td>0.6886</td>
</tr>
<tr>
<td>81</td>
<td>0.8686</td>
<td>103</td>
<td>0.6687</td>
</tr>
<tr>
<td>91</td>
<td>0.8440</td>
<td>4</td>
<td>0.5967</td>
</tr>
<tr>
<td>15</td>
<td>0.8125</td>
<td>120</td>
<td>0.5533</td>
</tr>
<tr>
<td>43</td>
<td>0.8092</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 17. Depleted Ecotopes of 'Upolu

<table>
<thead>
<tr>
<th>ECOTOPE NUMBER</th>
<th>INDEX OF DEPLETION</th>
<th>ECOTOPE NUMBER</th>
<th>INDEX OF DEPLETION</th>
</tr>
</thead>
<tbody>
<tr>
<td>173</td>
<td>0.9833</td>
<td>9</td>
<td>0.7454</td>
</tr>
<tr>
<td>37</td>
<td>0.9753</td>
<td>73</td>
<td>0.7208</td>
</tr>
<tr>
<td>102</td>
<td>0.9623</td>
<td>135</td>
<td>0.6650</td>
</tr>
<tr>
<td>110</td>
<td>0.9571</td>
<td>182</td>
<td>0.6648</td>
</tr>
<tr>
<td>30</td>
<td>0.9239</td>
<td>149</td>
<td>0.6631</td>
</tr>
<tr>
<td>176</td>
<td>0.9164</td>
<td>146</td>
<td>0.6497</td>
</tr>
<tr>
<td>115</td>
<td>0.8958</td>
<td>190</td>
<td>0.6299</td>
</tr>
<tr>
<td>133</td>
<td>0.8887</td>
<td>57</td>
<td>0.6275</td>
</tr>
<tr>
<td>20</td>
<td>0.8788</td>
<td>67</td>
<td>0.6122</td>
</tr>
<tr>
<td>6</td>
<td>0.8530</td>
<td>64</td>
<td>0.5915</td>
</tr>
<tr>
<td>27</td>
<td>0.8325</td>
<td>107</td>
<td>0.5711</td>
</tr>
<tr>
<td>123</td>
<td>0.8129</td>
<td>137</td>
<td>0.5619</td>
</tr>
<tr>
<td>141</td>
<td>0.8129</td>
<td>155</td>
<td>0.5247</td>
</tr>
<tr>
<td>88</td>
<td>0.7683</td>
<td>44</td>
<td>0.5159</td>
</tr>
<tr>
<td>83</td>
<td>0.7606</td>
<td>201</td>
<td>0.5077</td>
</tr>
<tr>
<td>101</td>
<td>0.7525</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
4.4 Determining the Natural Rarity of Ecotopes

Although it is appropriate to place highest priority on those ecotopes that are most depleted, it is also important to recognize that those ecotopes that are naturally rare are threatened to some degree by the mere fact of their rarity. Given that all places are somewhat threatened by the potential for human mismanagement, and given the constant threat of natural disturbances such as tropical cyclones, volcanic eruptions, and tsunamis, rarity is threatening. Equation 8 provides an index of relative natural rarity through the normalized ratio of the normative area of the individual ecotope type to that of the most common ecotope type.

\[
NR_i = \frac{A_{\text{max}} - A_i}{A_{\text{max}} + A_i}
\]

where

- \(NR_i\) is the index of natural rarity of a given ecotope type,
- \(A_i\) is the normative area of the ecotope type (the area of its actual and nominal distributions), and
- \(A_{\text{max}}\) is the normative area of the ecotope type with the largest normative area.

The ecotopes on Savai’i and ’Upolu with the largest normative areas were Lowland Rain Forest on lowland, gently sloping, Mulifanua substrates (17.3 % of Savai’i’s total area and its most depletionened ecotope) and Lowland Rain Forest on
lowland, gently sloping Salani substrates (21.8% of 'Upolu's total area). The majority of ecotopes on both islands have rarity indices in excess of 0.9000. The rarest ecotope on Savai'i is Mangrove on lowland, gently sloping, coastal alluvium. Six ecotopes are tied for the position of naturally least common on 'Upolu. These are Montane Rain Forest on lowland, steep, swamp alluviums; Lowland Rain Forest on montane moderate swamp alluviums; Coastal Rain Forest on lowland, moderately sloping, coastal alluviums; Fernland on lowland, moderately sloping, coastal alluviums; Swamp Forest on coastal, gently sloping, Lefaga substrates; and Herbaceous Marsh on coastal, gently sloping, Fagaloa substrates.\(^6\) Tables 18 and 19 provide lists of the 20 naturally rarest ecotopes for each of the two islands.

\(^6\)Note that four of these are marginal types, occurring along boundaries between major groups of landtypes (e.g., between montane and lowland landtypes).
Table 18. Naturally Rare Ecotopes of Savai’i

<table>
<thead>
<tr>
<th>ECOTOPE NUMBER</th>
<th>INDEX OF RARITY</th>
<th>ECOTOPE NUMBER</th>
<th>INDEX OF RARITY</th>
</tr>
</thead>
<tbody>
<tr>
<td>16</td>
<td>0.9998</td>
<td>101</td>
<td>0.9988</td>
</tr>
<tr>
<td>18</td>
<td>0.9995</td>
<td>121</td>
<td>0.9982</td>
</tr>
<tr>
<td>67</td>
<td>0.9995</td>
<td>127</td>
<td>0.9982</td>
</tr>
<tr>
<td>38</td>
<td>0.9991</td>
<td>24</td>
<td>0.9980</td>
</tr>
<tr>
<td>12</td>
<td>0.9989</td>
<td>70</td>
<td>0.9980</td>
</tr>
<tr>
<td>37</td>
<td>0.9989</td>
<td>88</td>
<td>0.9974</td>
</tr>
<tr>
<td>92</td>
<td>0.9989</td>
<td>17</td>
<td>0.9971</td>
</tr>
<tr>
<td>7</td>
<td>0.9988</td>
<td>73</td>
<td>0.9971</td>
</tr>
<tr>
<td>13</td>
<td>0.9988</td>
<td>40</td>
<td>0.9970</td>
</tr>
<tr>
<td>77</td>
<td>0.9988</td>
<td>72</td>
<td>0.9970</td>
</tr>
</tbody>
</table>
4.5 Calculating Priorities for the Conservation of Ecotopes

With indices of depletion and natural rarity in hand, an index of conservation priority was developed based on their weighted arithmetic mean. This index of conservation priority can be considered a rough estimate of threat since it is based on depletion and rarity.

\[ CP_i = \frac{2T_i + NR_i}{3} \]  \hspace{1cm} (9)
where

\[ CP_i \] is the index of conservation priority of an ecotope type.

An arithmetic mean was chosen instead of a geometric mean because it provides a less clumped distribution, with extreme values for any variable producing results that are more different from the mean. Furthermore, a vanishingly small or zero value for either variable does not produce a conservation priority of zero, a critical outcome in this case. Also note that the relative weights are easily justified, depletion being based on observed cases, while natural-rarity-as-threat is hypothetical. On the other hand, the exact weights are arbitrary (see the previous discussion of variable weights).

Twenty-four (27.6\%) of Savai'i's 87 ecotopes have conservation priorities in excess of 0.500. Sixty-three (49.2\%) of 'Upolu's 128 ecotopes have conservation priorities over 0.500. Tables 20 and 21 list and describe the ten ecotope types with the highest conservation priority scores for each island.
Table 20. Top Ten Conservation Priority Ecotope Types of Savai’i

<table>
<thead>
<tr>
<th>RANK</th>
<th>NO.</th>
<th>DESCRIPTION</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>60</td>
<td>Montane Rain Forest on lowland, moderately sloping Puapua substrates</td>
</tr>
<tr>
<td>2</td>
<td>74</td>
<td>Lowland Rain Forest on coastal, gently sloping Mulifanua substrates</td>
</tr>
<tr>
<td>3</td>
<td>10</td>
<td>Herbaceous Marsh on coastal, gently sloping, coastal alluvium</td>
</tr>
<tr>
<td>4</td>
<td>15</td>
<td>Herbaceous Marsh on lowland, gently sloping, coastal alluvium</td>
</tr>
<tr>
<td>5</td>
<td>43</td>
<td>Lowland Rain Forest on coastal, gently sloping Puapua substrates</td>
</tr>
<tr>
<td>6</td>
<td>91</td>
<td>Lowland Rain Forest on lowland, moderately sloping Mulifanua substrates</td>
</tr>
<tr>
<td>7</td>
<td>33</td>
<td>Volcanic Succession on lowland, moderately sloping Aopo substrates</td>
</tr>
<tr>
<td>8</td>
<td>124</td>
<td>Lowland Rain Forest on lowland, gently sloping Fagaloa substrates</td>
</tr>
<tr>
<td>9</td>
<td>4</td>
<td>Swamp Forest on coastal, gently sloping, swamp alluvium</td>
</tr>
<tr>
<td>10</td>
<td>120</td>
<td>Herbaceous Marsh on coastal, gently sloping Fagaloa substrates</td>
</tr>
</tbody>
</table>
Table 21. Top Ten Conservation Priority Ecotope Types of 'Upolu

<table>
<thead>
<tr>
<th>RANK</th>
<th>NO.</th>
<th>DESCRIPTION</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>37</td>
<td>Mangrove on lowland, moderately sloping, coastal alluvium</td>
</tr>
<tr>
<td>2</td>
<td>173</td>
<td>Ridge Rain Forest on coastal, gently sloping Fagaloa substrates</td>
</tr>
<tr>
<td>3</td>
<td>176</td>
<td>Ridge Rain Forest on coastal, moderately sloping Fagaloa substrates</td>
</tr>
<tr>
<td>4</td>
<td>102</td>
<td>Herbaceous Marsh on coastal, gently sloping Mulifanua substrates</td>
</tr>
<tr>
<td>5</td>
<td>30</td>
<td>Swamp Forest on lowland, gently sloping, coastal alluvium</td>
</tr>
<tr>
<td>6</td>
<td>133</td>
<td>Mangrove on coastal, gently sloping Salani substrates</td>
</tr>
<tr>
<td>7</td>
<td>115</td>
<td>Lowland Rain Forest on lowland, gently sloping Mulifanua substrates</td>
</tr>
<tr>
<td>8</td>
<td>27</td>
<td>Mangrove on coastal, moderately sloping, coastal alluvium</td>
</tr>
<tr>
<td>9</td>
<td>20</td>
<td>Mangrove on coastal, gently sloping, coastal alluvium</td>
</tr>
<tr>
<td>10</td>
<td>6</td>
<td>Swamp Forest on lowland, gently sloping, swamp alluvium</td>
</tr>
</tbody>
</table>

4.6 Conservation Priorities Among Regions

Note that the conservation priorities of hierarchically and geographically similar regions (e.g., islands, archipelagos, watersheds, landscapes) can now be compared by comparing the sums of CP, for each. This approach gives roughly equal weight to regions with a high number of low priority ecotopes and regions with a low number of high priority ecotopes.
\[ CP_{\text{region}} = \sum_{i=1}^{N} CP_i \]  

(10)

where

\( N \) is the number of ecotope types identified in the region.

When priority of individual ecotope types is more important than the number of ecotope types then the arithmetic mean value of the former should be used.

\[ CP_{\text{region}} = \frac{\sum_{i=1}^{N} CP_i}{N} \]  

(11)

Sometimes it is desirable to optimize for both ecotope diversity and the conservation priorities of the individual types. The coefficient of skewness of the distribution of the individual values may be used. Theoretical values of this coefficient range from -1 to 1 within a normal distribution, with 0 indicating no skewness of the distribution:
\[
S_m = \frac{\sum_{i=1}^{N} [CP_i - \bar{CP}_i]^2}{s^3N}
\]  \hspace{1cm} (12)

where

\(s\) is the variation and

\(S_m\) is the coefficient of skewness (Clark and Hosking 1986, pp. 86-87).

Since the skewness coefficient has a value that ranges from -1 to 1, adding 1 to it creates a revised coefficient with a value from 0 to 2. Using the sum of priorities approach (Equation 10) has the effect of producing a regional index that will be increased by a higher average conservation priority value and/or by more ecotope types. When multiplied by the revised skewness coefficient, the regional index theoretically can approach double its value if the distribution is highly skewed toward higher values, while the mean is offset by a few very low values. It also can theoretically approach zero if the distribution is highly skewed toward lower values while the mean is offset by a few very high values. A revised skewness coefficient of 1 (no skewness) will have no effect. Equation 13 illustrates this approach.

\[
CP_{\text{region}} = (S_m + 1)\sum_{i=1}^{N} CP_i
\]  \hspace{1cm} (13)
Finally, it is important to understand that the revised skewness coefficient will rarely deviate significantly from 1. When a regional index is significantly reduced by the skewness coefficient, the ecotope types with the highest individual conservation priority indices should be carefully considered, for their conservation indices will be very high.

Table 22. Comparative Conservation Priorities for Savai'i and 'Upolu

<table>
<thead>
<tr>
<th>METHOD</th>
<th>SAVAI'I</th>
<th>'UPOLU</th>
<th>RATIO 'UPOLU TO SAVAI'I</th>
</tr>
</thead>
<tbody>
<tr>
<td>EQUATION 10 (SUM OF PRIORITIES)</td>
<td>36.63</td>
<td>64.98</td>
<td>1.77</td>
</tr>
<tr>
<td>NUMBER OF ECOTOPES</td>
<td>87</td>
<td>128</td>
<td>1.47</td>
</tr>
<tr>
<td>EQUATION 11 (MEAN INDIVIDUAL PRIORITY)</td>
<td>0.42</td>
<td>0.51</td>
<td>1.21</td>
</tr>
<tr>
<td>STANDARD DEVIATION</td>
<td>.17</td>
<td>.19</td>
<td>n/a</td>
</tr>
<tr>
<td>EQUATION 12 (STANDARD SKEWNESS)</td>
<td>.10</td>
<td>.04</td>
<td>n/a</td>
</tr>
<tr>
<td>REVISED SKEWNESS</td>
<td>1.10</td>
<td>1.04</td>
<td>n/a</td>
</tr>
<tr>
<td>EQUATION 13 (OPTIMIZED, USING REVISED SKEWNESS)</td>
<td>40.29</td>
<td>67.57</td>
<td>1.68</td>
</tr>
</tbody>
</table>

'Upolu should receive higher priority for implementation of an ecotope conservation network. When resources are allocated, roughly one and a half times as
much emphasis should be placed on the 'Upolu network of reserves. This priority is based on 'Upolu’s larger number of ecotopes and their higher average conservation priority (depletion and rarity), adjusted slightly downward by Savai’i’s slightly higher ratio of high priority to low priority ecotopes (positive skewness).
5.1 Network Development

5.1.1 Designing the Network Cores

Once the priorities for ecotope conservation were established based on rarity and threat, it was necessary to establish a convention for including ecotope sites wholly or partially in a network of nature reserves. Other goals for the network included minimizing impacts on primary agricultural lands in customary tenure (regardless of cultivation status) (hereinafter referred to as "prime lands") and providing adequate stream buffers.

The first step in this process involved selecting ecotope sites for inclusion (in whole or in part) as nodes in the network. Nodes included only lands classified as actual (disturbed or undisturbed) native ecotopes. Lists of ecotope types were prepared for each island and sorted on the total actual area for each type. The area of prime land for each type was also calculated (Idrisi module CROSSTAB), as was the difference between the two numbers. These lists were examined to determine the best way to categorize ecotope types in terms of impacts of their conservation on prime land.
Finally, the lists were split into three categories. Category one included all ecotope types with 100 or fewer total Idrisi cells \(<225\) ha on Savai’i and \(<256\) ha on ‘Upolu). Category two included all remaining ecotope types with 500 or fewer cells remaining after the prime land cells were subtracted \(<1125\) ha on Savai’i and \(<1280\) ha on ‘Upolu). Category three included all the remaining ecotope types. This division between categories one and two was selected so that category one types collectively included no more than about 5\% of prime lands on both islands. The division between categories two and three was placed at the point at which ecotope types became common enough so each type in category three exceeded 1\% of the total land area of the island. The results of this process of creating categories are included in Tables 23 and 24. Note the significant discrepancy in percent of types between categories one and two for ‘Upolu and Savai’i. ‘Upolu’s ecotopes are more fragmented, and ‘Upolu has a higher percentage of rare types.

Table 23. Categories for Conservation Mapping of Ecotopes on Savai’i

<table>
<thead>
<tr>
<th>CATEGORY</th>
<th>% OF TYPES</th>
<th>TOTAL AREA (ha)</th>
<th>% OF NATIVE ECOTOPES AREA</th>
<th>% OF SAVAI'I LAND AREA</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>25.3</td>
<td>6846.8</td>
<td>7.4</td>
<td>4.0</td>
</tr>
<tr>
<td>2</td>
<td>62.1</td>
<td>27168.8</td>
<td>29.4</td>
<td>15.8</td>
</tr>
<tr>
<td>3</td>
<td>12.6</td>
<td>58485.4</td>
<td>63.2</td>
<td>33.9</td>
</tr>
</tbody>
</table>
Table 24. Categories for Conservation Mapping of Ecotopes on 'Upolu

<table>
<thead>
<tr>
<th>CATEGORY</th>
<th>% OF TYPES</th>
<th>TOTAL AREA (ha)</th>
<th>% OF NATIVE ECOTOPES AREA</th>
<th>% OF 'UPOLU LAND AREA</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>77.3</td>
<td>5611.5</td>
<td>12.8</td>
<td>4.8</td>
</tr>
<tr>
<td>2</td>
<td>15.6</td>
<td>13473.3</td>
<td>30.7</td>
<td>11.6</td>
</tr>
<tr>
<td>3</td>
<td>7.1</td>
<td>24627.2</td>
<td>56.1</td>
<td>21.3</td>
</tr>
</tbody>
</table>

Using Idrisi modules ASSIGN, OVERLAY, and RECLASS as well as prime lands masks for each island, Idrisi data layers were created for each island such that all category one cells were assigned a value of "1," all category two cells not also identified as prime land were assigned a value of "2," and all category three cells not also identified as prime land were labeled with their correct ecotope identification numbers. These images where then overlaid with vector files for rivers and roads (Idrisi module COLOR). The DIGITIZE sub-module within COLOR was then used to draw networks directly on the screen. All cells labeled "1" and "2" were automatically included. Significant fractions of all category three ecotope types were included with the added requirement that they serve as corridors to connect category one and two ecotopes when reasonable (e.g., without crossing roads). On Savai'i, an area of primary native Lowland Rain Forest was included because it contained a very high concentration of streams. The digitized networks were then relabeled as category three (Idrisi module RECLASS) and OVERLAY was used to cover the resulting network data layers with data layers consisting of all category one sites and
those category two sites that were not also identified as prime lands (see Figures 28 and 29). This last step repaired any errors resulting from the direct digitizing step.

The graphically developed networks served as the cores for the development of the final networks. Areas within the cores are intended to be managed as strict nature reserves. Tables 25 and 26 provide overviews of the two network cores.

Note that categories one, two, and three were mechanisms to be used only during the design of the network cores. All category one sites were included. All category two sites not also identified as prime lands were included. Representative examples of all category three types were included as sites within a partially-linking network. These categories were largely unrelated to conservation priority, and especially to its component variable of threat. Once the network cores were designed, these temporary categories were discarded. Implementation of conservation for the core areas should proceed according to the priorities of individual ecotope types as developed in Chapter 4.
Figure 28. Savai'i Nature Reserves Network Core
Figure 29. 'Upolu Nature Reserves Network Core
Table 25. Network Core Areas for Savai'i

<table>
<thead>
<tr>
<th>CATEGORY</th>
<th>% OF CATEGORY LANDS INCLUDED</th>
<th>% OF PRIME LAND INCLUDED</th>
<th>% OF TOTAL LAND AREA INCLUDED</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>100*</td>
<td>5.7</td>
<td>4.0</td>
</tr>
<tr>
<td>2</td>
<td>83.5</td>
<td>0*</td>
<td>13.2</td>
</tr>
<tr>
<td>3</td>
<td>53.4</td>
<td>0*</td>
<td>18.1</td>
</tr>
<tr>
<td>TOTALS</td>
<td>65.7</td>
<td>5.7</td>
<td>35.3</td>
</tr>
</tbody>
</table>

* by definition

Table 26. Network Core Areas for 'Upolu

<table>
<thead>
<tr>
<th>CATEGORY</th>
<th>% OF CATEGORY LANDS INCLUDED</th>
<th>% OF PRIME LAND INCLUDED</th>
<th>% OF TOTAL LAND AREA INCLUDED</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>100*</td>
<td>4.1</td>
<td>4.8</td>
</tr>
<tr>
<td>2</td>
<td>93.7</td>
<td>0*</td>
<td>10.9</td>
</tr>
<tr>
<td>3</td>
<td>37.6</td>
<td>0*</td>
<td>8.0</td>
</tr>
<tr>
<td>TOTALS</td>
<td>62.9</td>
<td>4.1</td>
<td>23.8</td>
</tr>
</tbody>
</table>

* by definition
5.1.2 Designing Buffers for the Networks

Once the core areas were designed, buffers were required. Idrisi module COSTGROW allowed the networks to be expanded by cellular increments in all directions. Ocean masks were then required to eliminate offshore increments.

A one cell buffer would range from 150 to 212 m wide on Savai’i and from 160 to 226 m wide on 'Upolu (based on sides and diagonals of cell sizes). Similarly, two cell buffers would range from 300 to 424 m wide on Savai’i and from 320 to 453 m wide on 'Upolu. Table 27 summarizes the differences between one and two cell buffers. Two cell buffers are recommended, as the minimum width of 300 m corresponds very well with the known penetration of edge effects for interior forest birds. Table 28 summarizes the kinds of lands included in the recommended networks.
Table 27. Buffer Development

<table>
<thead>
<tr>
<th>NETWORK AREA W/OUT BUFFERS (NB) (ha)</th>
<th>SAVAI'I</th>
<th>'UPOLU</th>
</tr>
</thead>
<tbody>
<tr>
<td>NB: % REDUCTION OF ALL LAND STOCKS</td>
<td>34.4</td>
<td>23.8</td>
</tr>
<tr>
<td>NB: % REDUCTION OF PRIME LAND STOCKS</td>
<td>5.7</td>
<td>4.1</td>
</tr>
<tr>
<td>NB: % REDUCTION OF NON-NATIVE ECOTOPE LAND STOCKS</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>NETWORK AREA ONE CELL BUFFERS (1C) (ha)</th>
<th>SAVAI'I</th>
<th>'UPOLU</th>
</tr>
</thead>
<tbody>
<tr>
<td>1C: % REDUCTION OF ALL LAND STOCKS</td>
<td>39.3</td>
<td>30.8</td>
</tr>
<tr>
<td>1C: % REDUCTION OF PRIME LAND STOCKS</td>
<td>18.4</td>
<td>11.9</td>
</tr>
<tr>
<td>1C: % REDUCTION OF NON-NATIVE ECOTOPE LAND STOCKS</td>
<td>5.8</td>
<td>6.0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>NETWORK AREA TWO CELL BUFFERS (2C) (ha)</th>
<th>SAVAI'I</th>
<th>'UPOLU</th>
</tr>
</thead>
<tbody>
<tr>
<td>2C: % REDUCTION OF ALL LAND STOCKS</td>
<td>43.4</td>
<td>37.0</td>
</tr>
<tr>
<td>2C: % REDUCTION OF PRIME LAND STOCKS</td>
<td>23.4</td>
<td>19.3</td>
</tr>
<tr>
<td>2C: % REDUCTION OF NON-NATIVE ECOTOPE LAND STOCKS</td>
<td>10.6</td>
<td>12.1</td>
</tr>
</tbody>
</table>
Table 28. Lands Included in the Two-cell (2C) Networks

<table>
<thead>
<tr>
<th>KINDS OF LAND INCLUDED</th>
<th>SAVAI'I AREA (ha)</th>
<th>'UPOLU AREA (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Core Areas, Undisturbed Native Ecotopes</td>
<td>55246.5</td>
<td>20743.7</td>
</tr>
<tr>
<td>Core Areas, Disturbed Native Ecotopes</td>
<td>3442.5</td>
<td>6620.2</td>
</tr>
<tr>
<td>Buffer Areas, Undisturbed Native Ecotopes</td>
<td>7560.0</td>
<td>4165.1</td>
</tr>
<tr>
<td>Buffer Areas, Disturbed Native Ecotopes</td>
<td>490.5</td>
<td>2511.4</td>
</tr>
<tr>
<td>Buffer Areas, Secondary Mesic Forest Ecotopes</td>
<td>526.5</td>
<td>463.4</td>
</tr>
<tr>
<td>Buffer Areas, Non-native Ecotopes</td>
<td>7546.5</td>
<td>8233.0</td>
</tr>
</tbody>
</table>

5.1.3 Adding Stream Buffer Corridors

The final step in formulating the networks for nature conservation was to include stream buffers for those cases when these fell outside the network lands as defined to this point. Recall that stream buffers should be at least 25 m wide (Hamilton and King 1983), but should vary considerably above that according to the local circumstances. Stream buffers one half cell wide would range from 75 to 106 m wide on 'Savai'i and from 80 to 113 m wide on 'Upolu (based on sides and diagonals of cell sizes). Stream buffers approaching this width would be more than adequate except in situations where the stream was itself identified as a high priority aquatic ecotope for conservation (outside the scope of this research). Buffers of less than this width could not be mapped using Idrisi cells of the size specified. Thus, the most straightforward approach to including additional stream buffers in the network was to simply plot the stream corridors outside the network as one cell buffers on the
assumption that a stream's average position bisected the cell. Obviously, on-the-ground planning should make minor adjustments in order to insure adequate buffer of at least 25 m. Table 29 summarizes the addition of lands to the networks as stream buffers. On Savai’i, stream buffers occupy 1503 additional ha of prime land (0.45% of the island total), while on 'Upolu, stream buffers occupy 1968.6 additional ha (0.65% of the island total).

Table 29. Lands Added to the Networks as Stream Buffers

<table>
<thead>
<tr>
<th>KINDS OF LAND ADDED</th>
<th>SAVAI'I AREA (ha)</th>
<th>'UPOLU AREA (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Buffer Areas, Undisturbed Native Ecotopes</td>
<td>1512.0</td>
<td>1574.4</td>
</tr>
<tr>
<td>Buffer Areas, Disturbed Native Ecotopes</td>
<td>6.8</td>
<td>837.1</td>
</tr>
<tr>
<td>Buffer Areas, Secondary Mesic Forest Ecotopes</td>
<td>247.8</td>
<td>611.8</td>
</tr>
<tr>
<td>Buffer Areas, Non-native Ecotopes</td>
<td>3224.2</td>
<td>5998.1</td>
</tr>
</tbody>
</table>

Figures 30 and 31 illustrate the final networks as developed using the methodology described to this point. By visual inspection, the networks are characterized by a few large, convoluted, contiguous areas of preserve and buffer lands in the uplands surrounded by many smaller preserves mainly in areas heavily influenced by human use and ecosystem conversion (e.g., along the coast) plus a network of narrow stream buffers in non-native ecotopes reaching from the streams' emergence from the network to the coast.
Figure 30. Savai'i Six Classes of Network Lands
Figure 31. 'Upolu Six Classes of Network Lands
5.1.4 Management Overview

Although detailed management planning for the proposed system of nature preserves in Western Samoa is outside the scope of the present research, it is necessary and useful to provide a framework for management planning, so that management plans will not violate the integrity of the network design. Six kinds of land have been included in the network. Each of these has a different genesis in the network supported by a different kind of reasoning. The approach to management for each of these must be developed separately, based on its own logic. Management approaches are discussed using the categories of protected areas established by the IUCN Commission on National Parks and Protected Areas (IUCN CNPPA 1978) and summarized by MacKinnon et al. (1978, pp. 15-26, especially the table on p. 21).

5.1.4.1 Core Areas of Undisturbed Native Ecotopes

These are the areas that dominate the networks and around which the networks were designed. The first goal of the reserve selection and network design planning process was to identify and include these areas, and the first goal of management must be to insure their adequate protection. When areas in this category are inadequate to conserve a particular ecotope type, then restoration lands are included under other categories with the intent of eventually adding them to this category. Lands in this category should be treated as Strict Nature Reserves, National Parks, or National Monuments/Landmarks (categories I - III) in which conservation of natural features, especially ecotopes, is the first goal of management. Strict Nature Reserve
status (category I) should be reserved for those sites that are most sensitive to human interference or that include threatened ecotopes and/or species. National Parks and National Monuments/Landmarks (categories II and III) are appropriate designations for reserves where human use is appropriate. The main difference is size, with the former being the larger. Monitoring for and managing to limit human impacts are critical for all three categories.

5.1.4.2 Core Areas of Disturbed Native Ecotopes

Fortunately, this is a rare type of land in the networks. Lands of this type are the highest priority for ecotope restoration, and management should be oriented primarily around protection and, to the extent possible, natural recovery. Active management should be focused mainly on the control and removal of non-native species and the repair of significant human disturbances of the substrate. Category IV (Managed Reserves) is generally appropriate, while categories II and III (National Parks, National Monuments/Landmarks) are appropriate only in cases where subsistence practices and other human uses will not interfere with recovery. Again, monitoring and managing human impacts are critical.

5.1.4.3 Buffer Areas of Undisturbed Native Ecotopes

Buffers of this type should be classified exactly like the core lands they adjoin. Recognize, however, that these lands inevitably are subject to significant edge effects, and more active management to control excessive degradation will be required.
5.1.4.4 Buffer Areas of Disturbed Native Ecotopes

This is the rarest type of land in the networks. Buffers of this type should be treated as high priority recovery lands and classified like the core areas they adjoin. Not only are these buffer lands subject to significant edge effects, but they will induce a weak edge effect extending into the core. These are high priority areas for ecotope recovery efforts. The recovery goal for these lands should be to reduce the level of disturbance in the buffer to the point that the edge effect is entirely contained in the buffer, thus protecting the core.

5.1.4.5 Buffer Areas of Secondary Mesic Forest Ecotopes

This is the second rarest type of land in the networks. These buffers should be treated exactly like buffers of disturbed native ecotopes except that the urgency of the recovery effort is even higher. Ecotope restoration requires more active management, including significantly more active rehabilitation activity and relatively less reliance on passive recovery (Cairns 1986).

5.1.4.6 Buffer Areas of Non-Native Ecotopes

This is one of the two most common types of buffer lands for network cores, and the most common type of stream buffer (64.6% on Savai’i and 66.5% on 'Upolu). These two sub-classes should be treated separately.
Non-native ecotope buffers are found most often around the smaller and more isolated satellite reserves of native ecotopes, and thus typically the rarest ecotope types. Thus, this weakest of buffer types is found most often around the most vulnerable of reserves. The matter is further complicated by the very high probability that native ecotopes probably cannot be completely restored (replaced) in the buffer due both to lack of adequate scientific knowledge and to cultural resistance to the conversion. These buffers will require the most intensive management if they are to serve as buffers at all, and the inevitable edge effects extending into the core from the buffer must be monitored and controlled.

On the other hand, stream buffers of non-native ecotopes may serve their purposes very well. The IUCN CNPPA classification does not include a category of lands designated primarily to protect watershed values and prevent erosion (MacKinnon et al. 1978, p. 21), yet these are the universal management objectives for stream buffers. These objectives can be accomplished through relatively low intensity management practices. In many cases, exclusion of herbicides and fertilizers and prevention of clear-felling and grazing will be adequate management objectives for non-native ecotope buffers for streams.

Lands in both sub-classes of non-native buffers should be treated as transitional between a landscape of essentially unregulated human use and the stream or core area intended for protection by the buffer. In the case of native ecotope cores, the buffer
restoration objective should be to replace non-native ecotopes with pseudo-native ecotopes or intensively managed non-native systems largely capable of containing the edge effect. For streams outside of the core areas, non-native buffers should be managed to allow all human activities that do not significantly degrade stream ecotopes.

5.2 Network Description

Category V of the IUCN CNPPA classification is the Protected Landscape. Although this category generally is understood to include various cultural and scenic conservation objectives, it also includes the important, if not primary, objective of conserving the ecotopes of the landscape. From the perspective of landscape ecology, where the landscape is the meta-ecosystem of interacting ecotopes, the goal of landscape conservation is ecological stability defined to include not only conservation of ecosystems but conservation of their ability to interact. The networks of cores and buffers were designed, if not to fully implement, at least to make possible, this ecological stability at the landscape level. Several of the categories of buffers were also designed to sustain various human uses, and these uses (especially hunting, gathering of forest products, and very low intensity swidden gardens) may even extend into the cores where they are not contrary to ecosystem conservation.

Studying Figures 30 and 31 with the design guidelines from Chapter 3 in mind does not yield any clear sense of whether or not the design objectives implicit or
explicit in conservation biology and landscape ecology were met. Can more objective measures of success be developed? Before this can be attempted, the networks themselves must be described more objectively.

5.2.1 Area

The first and simplest measure of the networks was determination of the areas of the individual composite map units in the network cores (Figures 28 and 29), that is, of the units of contiguous cells (polygons) in the cores. Idrisi module RECLASS was used to assign all core cells a value of one, then Idrisi module GROUP was used to assign a unique identifier to all of the resultant polygons. Idrisi module RECLASS was used to assign a value of zero to all polygons that should have been set to zero, but were given non-zero values because they were entirely enclosed by non-zero polygons. Idrisi module AREA was then used to create data files containing area information for each of the polygons. Table 30 provides information on the areas of the individual polygons.
Table 30. Areas of the Individual Polygons in the Conservation Network Cores

<table>
<thead>
<tr>
<th></th>
<th>SAVAI'I</th>
<th>'UPOLU</th>
</tr>
</thead>
<tbody>
<tr>
<td>NO. OF POLYGONS</td>
<td>83</td>
<td>122</td>
</tr>
<tr>
<td>MIN. VALUE (ha)</td>
<td>2.25</td>
<td>2.25</td>
</tr>
<tr>
<td>MAX. VALUE (ha)</td>
<td>48501</td>
<td>13785.59</td>
</tr>
<tr>
<td>MEAN (ha)</td>
<td>714.06</td>
<td>225.42</td>
</tr>
<tr>
<td>MEDIAN (ha)</td>
<td>20.25</td>
<td>15.35</td>
</tr>
<tr>
<td>MODE (ha)</td>
<td>2.25</td>
<td>2.25</td>
</tr>
<tr>
<td>STANDARD DEV.</td>
<td>5319.22</td>
<td>1327.00</td>
</tr>
<tr>
<td>SKEWNESS</td>
<td>9.06</td>
<td>9.28</td>
</tr>
<tr>
<td>KURTOSIS</td>
<td>82.36</td>
<td>92.62</td>
</tr>
</tbody>
</table>

The most obvious characteristic of the data described in Table 30 is that the distribution is anything but normal. The minimum value is also the mode, and almost all of the polygons are very small. The median and mean values are much closer to the minimum/mode than to the maximum. Using Pearson's coefficient of skewness, a skewness value of zero indicates no asymmetry in the distribution around a measure of central tendency (Clark and Hosking 1986, pp. 86-87). For normally distributed data, the skewness value should not exceed 1.0. Kurtosis measures how pointed or flat a frequency distribution appears. Normally distributed data would have a kurtosis value close to 1.0. Negative kurtosis indicates a flattened curve, while positive kurtosis indicates a pointed curve (Clark and Hosking 1986, p. 87). The data for polygon areas are strongly positively skewed (the majority of the values are well...
below the mean) and strongly leptokurtic (very sharply peaked, the highest values being much higher than the mean).

Only a very few polygons can be considered very large. The very large polygons are cases where the hybrid rule-based and graphical approach to the generation of networks succeeded. The very small polygons are evidence of fragmentation in the landscape that could not be bridged graphically without violating the rules under which the networks were developed.

5.2.2 **Perimeter and Shape**

Another measure of the networks was determination of the perimeters of the individual composite map units in the network cores. The grouped and reclassified images from the previous determination were used. Idrisi module PERIM was then used to create data files containing perimeter information for each of the polygons. Table 31 provides information on the perimeters of the individual polygons.
Table 31. Perimeters of the Individual Polygons in the Conservation Network Cores

<table>
<thead>
<tr>
<th></th>
<th>SAVAI'I</th>
<th>'UPOLU</th>
</tr>
</thead>
<tbody>
<tr>
<td>NO. OF POLYGONS</td>
<td>83</td>
<td>122</td>
</tr>
<tr>
<td>MIN. VALUE (m)</td>
<td>600</td>
<td>640</td>
</tr>
<tr>
<td>MAX. VALUE (m)</td>
<td>429000</td>
<td>212480</td>
</tr>
<tr>
<td>MEAN (m)</td>
<td>10333.73</td>
<td>6121.97</td>
</tr>
<tr>
<td>MEDIAN (m)</td>
<td>2400</td>
<td>2080</td>
</tr>
<tr>
<td>MODE (m)</td>
<td>1500</td>
<td>640</td>
</tr>
<tr>
<td>STANDARD DEV.</td>
<td>47012.14</td>
<td>20518.23</td>
</tr>
<tr>
<td>SKEWNESS</td>
<td>8.82</td>
<td>8.80</td>
</tr>
<tr>
<td>KURTOSIS</td>
<td>79.42</td>
<td>86.36</td>
</tr>
</tbody>
</table>

The distributions of perimeter data match very closely those of area data. Perimeter data alone is of little interest however. Much more useful indices based on area and perimeter are available. These are the indices of shape. Generally, two indices of shape are discussed in the literature. The first and older of these is the roundness index with its variants (Austin 1984; Forman and Godron 1986, p. 188; Game 1980; Patton 1975; Selkirk 1982, pp. 53-57):
\[ R = \frac{2\sqrt{\pi A}}{P} \]  

(14)

where

- \( R \) is the Roundness Index,
- \( A \) is the area in \( m^2 \), and
- \( P \) is the perimeter in m.

Most authors present this equation in inverted form, with \( P \) as the numerator, but in the form used here, with \( P \) as the denominator, roundness varies directly with the index, from a circle with a roundness index of 1.0 to shapes very far from round with indices approaching zero. A square has an index of 0.88, a rectangle of 1 x 100 units has an index of 0.17, and a rectangle of 1 x 1,000,000 units has an index of 0.002. Table 32 summarizes the roundness indices for the network polygons of Savai'i and 'Upolu.
Table 32. Roundness of the Individual Polygons in the Conservation Network Cores

<table>
<thead>
<tr>
<th></th>
<th>SAVAI'I</th>
<th>'UPOLU</th>
</tr>
</thead>
<tbody>
<tr>
<td>MIN. VALUE</td>
<td>0.18</td>
<td>0.20</td>
</tr>
<tr>
<td>MAX. VALUE</td>
<td>0.89</td>
<td>0.89</td>
</tr>
<tr>
<td>MEAN</td>
<td>0.68</td>
<td>0.68</td>
</tr>
<tr>
<td>MEDIAN</td>
<td>0.88</td>
<td>0.68</td>
</tr>
<tr>
<td>MODE</td>
<td>0.89</td>
<td>0.88</td>
</tr>
<tr>
<td>STANDARD DEV.</td>
<td>0.16</td>
<td>0.16</td>
</tr>
<tr>
<td>SKEWNESS</td>
<td>-0.57</td>
<td>-0.45</td>
</tr>
<tr>
<td>KURTOSIS</td>
<td>-0.05</td>
<td>-0.16</td>
</tr>
</tbody>
</table>

Note that most polygons were slightly closer to round than not, and that the polygons with the highest roundness indices were those with the lowest areas (single cells) while the largest polygons had the lowest roundness indices. Only the very largest had indices below 0.50. In other words, roundness tended to vary inversely with size which varied directly with the success of the rule-based, graphical solution. Note also that the distribution of roundness is nearly normal, with Savai'i showing slightly more tendency toward rounder polygons.

Another index of shape is the fractal dimension (LaGro 1991, Loehle 1991, Longly and Batty 1989, Rex and Malanson 1990, Turner 1989a). This is actually a measure of the convolution of the perimeter of a polygon. The fractal dimension can vary from 1.0 to 2.0, with highly convoluted perimeters having fractal dimensions
approaching 2.0, while very simple polygons have fractal dimensions approaching 1.0.\(^1\) The formula for fractal dimension is given:

\[
D = \frac{2(\log P)}{\log A}
\]  
(15)

where

= the fractal dimension.

Table 33 summarizes the fractal dimensions for the network polygons of Savai’i and ‘Upolu.

\(^1\)Technically, a fractal is a shape with a self-similar boundary. In other words, the boundary of the shape is defined by a repeating form that, upon magnification, can be seen to be composed of the same form at a smaller scale that, upon further magnification, can be seen to be composed of the same form at an even smaller scale and so on. A perfect fractal has a dimension of 2.0, and the boundary occupies or fills 100% of the space defined by the equation(s) that define the fractal shape. The boundary is perfectly convoluted within the limits set by the descriptive equation(s). At this point, the boundary composed of one-dimensional line segments can be said to be, in aggregate, exactly two-dimensional in that it perfectly fills all of the plain that it has access to. The fractal dimension of a non-fractal boundary is an approximate measure of boundary convolution based on the theory that more convoluted boundaries approach being fractal in nature. Foundation references on fractals and fractal dimensions include Barnsley et al. (1986), Mandelbrot (1982), and Peitgen and Richter (1986).
Table 33. Fractal Dimensions of the Individual Polygons in the Conservation Network Cores

<table>
<thead>
<tr>
<th></th>
<th>SAVAI'I</th>
<th>'UPOLU</th>
</tr>
</thead>
<tbody>
<tr>
<td>MIN. VALUE</td>
<td>1.22</td>
<td>1.22</td>
</tr>
<tr>
<td>MAX. VALUE</td>
<td>1.32</td>
<td>1.32</td>
</tr>
<tr>
<td>MEAN</td>
<td>1.28</td>
<td>1.28</td>
</tr>
<tr>
<td>MEDIAN</td>
<td>1.27</td>
<td>1.27</td>
</tr>
<tr>
<td>MODE</td>
<td>1.28</td>
<td>1.27</td>
</tr>
<tr>
<td>STANDARD DEV.</td>
<td>0.02</td>
<td>0.02</td>
</tr>
<tr>
<td>SKEWNESS</td>
<td>0.70</td>
<td>0.17</td>
</tr>
<tr>
<td>KURTOSIS</td>
<td>0.46</td>
<td>2.85</td>
</tr>
</tbody>
</table>

All polygons exhibit fractal dimensions closer to 1.0 than 2.0. That is, all polygons have relatively smooth perimeters. Mean, median, and mode values are nearly identical, and skewness and kurtosis values are relatively low, indicating nearly normal distributions. The rule-based, graphical solution tended to produce relatively smooth boundaries with no significant correlation between a polygon's boundary smoothness and its size.

5.2.3 Diversity

Measurements of area and shape are measurements of individual polygons. There are measures of the aggregate of polygons based on variation among their attributes, in this case, the ecotopes they contain. For these measures, then, it is necessary to subdivide the network cores according to ecotope types.
The simplest measure of aggregate, non-spatial variation is richness, or the simple number of ecotopes included in the network cores. For Savai‘i, 87 types were included, while for 'Upolu, 128 were included. Since 100% of all ecotope types were included in each case, the relative richness or the richness of the sample (the network core) compared to the richness of the population (the actual ecotopes) in each case was 100% (Turner 1989a). The relative richness of the core compared with the normative landscape was only slightly lower, with the difference attributable to the missing and therefore unknown ecotope types (vegetation - landtype pairs).

In 1949, Shannon and Weaver published their work on information theory. This work included an index of diversity as a measure of information content. This index has been widely adapted as a measure of biological and ecological diversity (MacArthur 1965; Whittaker 1975, pp. 94-104) and has recently been adapted as a measure of ecosystem diversity in a landscape (O’Neill, Krummel et al. 1988; Turner 1989a, 1990; Turner, O’Neill, et al. 1989). The formula is commonly given as:

\[ H = - \sum_{i=1}^{N} (PE_i)\ln(PE_i) \]  
\[ 16 \]  

where

\[ H \]  is the diversity index,
PE is the proportion of the landscape or network occupied by the ith ecotope, and

N is the number of ecotopes in the landscape or network.

An ideal reserves network would be as diverse as the normative landscape it theoretically is nested in. Thus, a measure of success based on diversity would be the proportion of the ecotope diversity in the normative landscape captured by the network, or the relative diversity of the network:

\[ H_{nl} = \frac{100(H_n)}{H_l} \]  \hspace{1cm} (17)

where

- \( H_{nl} \) is the relative diversity of the network compared to the normative landscape,
- \( H_n \) is the diversity index of the network, and
- \( H_l \) is the diversity index of the normative landscape.

Another way of looking at the same question is to ask whether the core captured a significant share of the diversity of the actual native ecotopes of the landscape. The same equation is used

where
\(H_{ra}\) is the relative diversity of the core compared to the actual native ecotopes in the landscape (replacing \(H_{a}\)), and \(H_{r}\) is the diversity index of the actual native ecotopes in the landscape (replacing \(H_{r}\)).

Table 34 summarizes the diversity information for Savai'i and 'Upolu and their preserve networks (note that since Savai'i and 'Upolu have neither the same area nor the same abiotic environments, comparisons in Table 34 should be confined within columns).

<table>
<thead>
<tr>
<th></th>
<th>SAVAI'I</th>
<th>'UPOLU</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>DIVERSITY OF THE NORMATIVE LANDSCAPE</strong></td>
<td>163.43</td>
<td>102.61</td>
</tr>
<tr>
<td><strong>DIVERSITY OF THE NATIVE ECOTOPES IN THE ACTUAL LANDSCAPE</strong></td>
<td>127.62</td>
<td>81.12</td>
</tr>
<tr>
<td><strong>NETWORK DIVERSITY</strong></td>
<td>120.07</td>
<td>67.77</td>
</tr>
<tr>
<td><strong>NETWORK DIVERSITY RELATIVE TO THE NORMATIVE</strong></td>
<td>73.47</td>
<td>66.05</td>
</tr>
<tr>
<td><strong>NETWORK DIVERSITY RELATIVE TO THE ACTUAL</strong></td>
<td>94.08</td>
<td>83.54</td>
</tr>
</tbody>
</table>

In both cases, the networks captured well over 50% of the diversity of the normative landscapes and nearly all of the diversity of the native ecotopes in the actual landscapes. The lower relative network diversity values for 'Upolu can be
attributed to the more fragmented actual landscape of that island, and the limitations such fragmentation placed on the graphical solution.

5.2.4 Distribution and Autocorrelation

For groups of objects, the various spatial measures listed in Chapter 2 generally require that the objects be of roughly normally distributed sizes or weights and that they be roughly randomly distributed in the landscape (e.g., the nearest neighbor statistic). Radical deviation from these rules prohibits the use of most of the indices. However, since deviation from the rules was considered desirable (we wanted networks of preserves as large and as connected as possible), then a measure of the deviation itself may be a measure of success. The spatial autocorrelation for the two networks was determined. For Savai’i, the Moran’s I spatial autocorrelation statistic for network core cells was 0.93, while for ’Upolu it was 0.86. Both high values for autocorrelation can be taken as indicators of success. As expected, the polygons in the ’Upolu network core are smaller and less well connected than those of Savai’i.

Since none of the existing indices of spatial distribution seemed useful to the present research, one was devised. It is possible to calculate the extension of the reserve network core into the total landscape of an island. This "index of extension" is expressed as the normalized ratio of the mean distance of the average point on the island from the nearest extension of the network core to the mean distance of the
average point on the island from the centroid of the island (the standard radius or
distance; Clark and Hosking 1986, pp. 100-106):

\[ E = \frac{D_c - D_e}{D_c + D_e} \]  \hspace{1cm} (18)

where

- \( E \) is the index of extension,
- \( D_c \) is the distance of a point from the centroid of the island, and
- \( D_e \) is the distance of a point from the nearest extension of the network core.

Using this formula, if the network core occupies a mathematical point in the center of a circular island, its index of extension will be exactly zero. That is, as the mean distance to the core approaches the mean distance to the centroid of the island, the index approaches zero. As the network core approaches coincidence with the entire island, regardless of the island's shape, then the index of extension approaches one. In other words, as the mean distance to the core approaches zero, the index of extension approaches one.

Note that the network core can occupy much less than the entire island and still have a high index of extension. If the core consists of many arms and/or
satellites so that few points on the island are far away, the index will approach one. Thus, the index of extension can be increased by higher values for indices of boundary convolution (the fractal index) or fragmentation of the core (indicated by area distributions).

Determining the mean distance to the centroid of the islands was accomplished simply using Idrisi module CENTER to determine the standard distance. The mean distance to the reserve network core was determined by using Idrisi module DISTANCE to calculate the mean distance from the core for each cell in the image, then RECLASS was used to lump these values into classes 400 m wide. The area in hectares for each class was determined using Idrisi module AREA, and the mean value for the average hectare was then determined:

\[
\overline{D_e} = \frac{\sum_{i=1}^{N} A_i D_i}{\sum_{i=1}^{N} A_i} \tag{19}
\]

where

- \( A_i \) is the area of the \( i \)th class,
- \( D_i \) is the mean distance to the core for the members of the \( i \)th class, and
- \( N \) is the number of classes.

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The network extension indices are 0.90 for Savai‘i and 0.78 for ‘Upolu indicating that both networks are highly extended into the landscapes of the two islands. Recall that roundness indices were relatively high and fractal indices were relatively low for the networks, so little extension was produced by boundary convolution. Recall also that the distribution of core areas was strongly leptokurtic and strongly skewed toward smaller reserves. Thus the high indices of extension are explained mainly by the spatial distribution of unconnected small reserves and less by the convolution of boundaries of the largest reserves.

5.2.5 Connectivity

Since one goal of the rule-based graphical solution was to generate connectivity among as many polygons as possible, a measure of connectivity seems appropriate. Unfortunately, network indices of connectivity and circuitry are based on being able to distinguish between links and nodes (the connectors and the connected) (Forman and Godron 1986, pp. 417-420). These indices typically treat nodes as points. Thus, indices of connectivity and circuitry cannot be applied very constructively to the proposed network cores which are made up of patches selected to be as connected as possible given a rule-based approach.

Another stochastic measure of connectivity requires that polygons or cells be more-or-less randomly distributed. Percolation theory states that in a random grid, an average of 59% of all cells must be available in order for an event to percolate
through the grid on available cells (typically based on adjacency and allowing corner cells in a rectangular grid, i.e., King's case adjacency) (Gardner et al. 1989; Gardner and O'Neill 1991; O'Neill, Milne, et al. 1988; Stauffer 1985; Turner, Gardner, et al. 1989). In terms of landscapes, a plant species requiring a given substrate to propagate would require an average of 59% of the landscape be randomly occupied by that substrate in order to traverse the landscape by propagation between adjacent cells.

The percentages of land in the cores are 35.3% and 23.8% for Savai'i and 'Upolu respectively. However, even if these figures were over 59%, the stochastic prediction of the percolation statistic would fail, because the network cores were not drawn randomly. They do not cross circum-insular roads, for example. Neither of the networks is completely connected as a result of the rule-based process (and indirectly, of the influence of roads). Thus, in a landscape where nature reserves are not randomly distributed, percolation fails as a useful measure of potential connectivity. No measure of connectivity seems useful.

5.3 Network Generalization

So far, the process for network generation has focused on the particular. Very specific rules were used at each step along the way, and these were designed to meet the requirements of the local situations on the islands of Savai'i and 'Upolu in Western Samoa. All reporting on the results of the process has featured description.
of the networks generated on the two islands, and, in some cases, the end results were strongly configured by the geography of the islands (e.g., the prevention of interior-to-coast linkages by circum-insular roads). Can the two networks be generalized to the point that a useful network model emerges for other tropical forested islands or even for other kinds of regions? The answers would seem to be yes for most tropical forested islands and generally no for other kinds of regions.

5.3.1 The Influence of Size and Shape

Savai‘i and 'Upolu are relatively compact and round as are most tropical forested islands. They have peninsulas and bays and are to some extent elongated, but these disappear as features on maps using very small scales, long before the islands themselves disappear. Also, they are higher in their centers than on their coasts. The natural distribution of ecotopes is strongly influenced by the surrounding ocean, the elevated island centers, and the patchiness of the substrate. These features bode well for being able to generalize the network model to other islands.

The shape, size, and extension of the network cores on Savai‘i and 'Upolu seem to be determined by these features of shape and size. On both islands, the network cores resemble montane glaciers, dominating the central massifs and extending arms into the lowlands. These are then surrounded by small reserve satellites that also tend to cluster along the coasts. Neither of the networks manages a mountain-top to coast arm, for all possible avenues are interrupted by circum-insular
roads. However, careful evaluation reveals no direct causative mechanism between
general island size or shape and the resultant networks.

5.3.2 The Influence of Culture

On the other hand, numerous aspects of the human and environment interface
are strongly deterministic for the network cores. For example, because road building
is much easier at the lower coastal elevations and given milder coastal topography,
the first road built on most islands is along the coast, and circum-insular roads are
common. For exactly the same reasons, the clearing of forests and the conversion of
other ecotopes proceeds more rapidly in the coastal zone and more slowly in the high
interiors. Because the oceans represent commerce and access to ocean products, and
because people build villages, till the soil, and plant gardens best on flatter and richer
lands, the coasts tend to be the preferred areas for settlement. Coastal ecotopes
consequently are both more rare and more threatened in general. These influences
tend to make feasible the generalization of the network models to tropical forested
islands with a few notable exceptions. These are the makatea islands and the older
coral atolls. In the former case, the makatea results in a band of relatively intact
forest around the island edge while human habitations and gardens tend to be confined
to the interior. In the case of older coral atolls, human activities and ecotope
remnants are patchily distributed in the motus, while the island interiors are
dominated by one or more lagoons.
Because neither environment nor human activity is separately deterministic, and because the combination is strongly influential on factors such as the distribution of roads and the extent to which some ecotope types are preferentially converted, the shape of the model cannot be generalized reasonably to regions where the human-environment interactions are markedly different from those on most tropical forested islands.

5.4 Process Generalization: Regional Ecosystem Analysis and Landscape Conservation (REAL Conservation)

Although the model itself cannot be generalized usefully outside the case of tropical forested islands, the process whereby it was derived can be generalized easily and profitably for application to virtually any landscape. The following outline summarizes the process as developed during the current research. Important or key points are underlined for emphasis.

5.4.1 Process Outline

I. Determine the goals and rules that will drive the process (e.g., in the current research, the design goal was to include representative examples of all native ecotopes and the main design rule was that prime land in customary tenure was to be excluded if at all possible).

II. Design the reserve networks and recommend management parameters.

A. Generate Foundation Data.
1. Data Types:
   
a. Current vegetation, classified hierarchically and mapped at least to the level of formation

b. Current vegetation nativity and disturbance regimes

c. Substrate (either soils or geology)

d. Topography (either digital elevation model or contours)

e. Moisture regime (potentially extractable from soils data; not used in the current research)

f. Land tenure and/or other data sets selected on the basis of process goals and rules

2. Data Rules:

   a. Data must be collected and mapped at comparable scales.

   b. Data confidence regions should be mapped for each data type if possible.

B. Develop a Geographical Information System.

   1. Select hardware and software.

      a. Hardware and software selection must be capable of supporting the project while at the same time being relatively accessible to potential users of the product.

      b. Requirements for conversion of data from other formats should be evaluated in advance, as these may be
deterministic when critical data is in a format that is only accessible from certain platforms.

2. Load available computer data and digitize the rest.

3. Describe the data sets, as characteristics of the data will be limiting.

C. Define Ecosystems (ecotopes).

1. Define landtypes choosing topo-edaphic data that correlate well with vegetation.

2. Correlate vegetation and landtypes, thus defining actual ecotopes.

3. Using Bayesian inference, develop probabilistic relationships between vegetation and landtypes.

4. Map normative vegetation from landtypes and overlay actual vegetation.

5. Map nominal and actual ecotopes.

D. Determine Ecotope Priorities for Conservation.

1. Determine the levels of threats to ecotopes by comparing actual and normative distributions.

2. Determine the degrees of natural rarity of ecotopes by comparing relative normative distributions.

3. Optionally, evaluate the relative priority of regions for conservation.
E. Define Network Cores.

1. Determine the points in the continuum of data values where project goals are superseded by project rules. For example, in the current research, sites for the rarest (actual) ecotopes were automatically included in the networks (a goal) up to the point that the rule prohibiting the inclusion of prime land in customary tenure was significantly violated. Using goals and rules, include sites for the rarest (actual) ecotopes in the network core(s).

2. For less rare (actual) ecotopes, devise a graphical solution so that adequate pieces of more common ecotopes tend to tie the network together with high quality corridors. The graphical solution should result in inclusion of sites for all (actual) ecotopes in the network, assuming this is a goal.

F. Define Network Buffers.

1. Buffers should be designed around all of the core(s).

2. Buffers should be wide enough to absorb edge effects before these can penetrate the core(s). In the present research, the buffers were designed by expanding the network core(s) by two raster cells, resulting in a minimum buffer width conveniently close to the maximum edge effect reported by Lovejoy et al. (1983, 1984, 1986) for tropical rain forests.
3. **Add stream buffers.**

**G. Develop Management Parameters.**

1. **The networks (cores and buffers) should be divided into management categories** (e.g., strict nature reserve, national landmark, etc.).

2. Management parameters for the network categories should be developed with the highest emphasis on conservation of the core ecotopes, but recognizing that human uses for some of the lands are inevitable and, in many cases, desirable.

### 5.4.2 Process Rationale Revisited

The process developed in this research and generalized in the outline above can be called "Regional Ecosystem Analysis and Landscape Conservation," a descriptive name that has the fortunate acronym, "REAL Conservation." The purpose of REAL Conservation is to conserve the potential for landscape-level ecological stability based on the theory of landscape ecology and incorporating principles of conservation biology. REAL Conservation does not require a complex understanding of material, energy, and organism flows among ecotopes. Instead, it substitutes the surrogate principle of conserving ecotopes in networks that, if the theory of landscape ecology is valid, results in the conservation of inter-relations among ecotopes in the landscape.

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REAL Conservation is based on ecosystems. The logic behind conserving ecosystems at one scale (ecotopes) in an effort to conserve ecosystems at the next larger scale (landscapes) is well developed. On the other hand, there is nothing about this process that precludes or is pejorative to the inclusion of other conservation targets as well. For example, adding a data layer for threatened or endangered species (T/E species) is perfectly sensible. Once included, these data can drive inclusion of habitat for such species in a very straightforward fashion. The presence of T/E species can be used to assign priorities to ecotopes for inclusion in the networks, and T/E sites themselves can be included as the result of goals and/or rules. Both options are highly desirable.

On the other hand, attempts to develop conservation land plans without including ecosystems must ultimately fail at or above the landscape level, hence the serendipity of the acronym. The REAL Conservation approach was developed in hopes that by systematically targeting ecotopes for conservation such failures could be prevented. But will it work?
CHAPTER 6

EVALUATION AND CONCLUSIONS

6.1 Innovations in the REAL Conservation Approach

Before evaluating the success of the current research, the innovations on which it is based ought to be enumerated. These are either the foundations of success or the most likely sources of failure. Success in the research will tend to validate these innovations and failure will render them suspect, although failure can also result from the poor application of perfectly valid tools.

6.1.1 The Ecologically Stable Landscape

Although the notion of sustainable development is very much on the public agenda, very few authors have undertaken to synthesize a definition for an ecologically sustainable (stable) landscape, treating the latter as an ecosystem itself comprised of component ecosystems (but see Forman 1990b). Chapter 1 contains such a synthesis based on a review of modern ecosystem concepts. The conclusion is that an ecologically stable landscape can be defined as one where the patterns and processes of component ecotope interaction are changing relatively slowly and where entropy gradients are shallow. In an ecologically stable landscape, component ecotopes will persist without simplification or collapse, and the ordinary processes of material and biological interaction among them will not change rapidly.
6.1.2 The Theory of Landscape Ecology

The Theory of Landscape Ecology seems to be implicit in every document generated by the discipline, but the current research yielded no case of its explicit statement. This is provided, therefore, in Chapter 1. The Theory of Landscape Ecology holds that the biological and material interactions among ecosystems are highly (often mainly) influenced by their relationships in geographical space. A conservation corollary states that measuring, modelling, and preserving these spatial relationships provides a useful, approximating approach to conserving the interactions among the ecosystems (ecotopes) of landscapes, and thus, the stability of the landscapes themselves.

6.1.3 Classifying and Mapping the Vegetation of Western Samoa

An integral and essential part of this research was the generation of a map of the existing vegetation of Western Samoa. No such map had ever been generated before, although a poorly conceptualized and implemented map of lower elevation forest resources had been generated in the late 1970s (Olsen and Co. 1978). The mapping project required the development, based on the literature, of an a priori classification of the vegetation of Western Samoa which was then extensively modified and clarified in the field. The classification and map potentially stand alone as significant contributions to the state-of-knowledge about Pacific island ecology.
6.1.4 Evaluation of Approaches to the Use of SPOT Satellite Data

SPOT Satellite data was used to map the vegetation of most of the island of Savai‘i. Various approaches to contrast enhancement and classification were tested, and the best and most productive technique was selected. Contrary to expectations, image classification did not prove to be productive, but contrast enhancement to identify the edges of vegetation units proved to be very valuable indeed. The contrast enhancement method that proved to be the most useful was a simple contrast stretch of masked normal data with the resulting data range divided into roughly equally populated classes. This very simple approach produced more useful boundaries than the more complex alternatives commonly discussed in the contemporary literature.

6.1.5 Defining and Mapping the Ecotopes of Western Samoa

Vegetation is commonly defined and mapped as part of regional conservation efforts, and more ambitious efforts sometimes include attempts to classify and map ecosystems. The present research includes a classification and map of the ecotopes of Western Samoa defined systematically and consistently as the common occurrences of landtypes and vegetation, in itself a contribution to the state-of-knowledge. Furthermore, the present research also includes an innovative application of Bayesian inference to develop probability relationships between vegetation and landtype so that:

a. where native vegetation is missing or severely altered, the most probable class(es) of vegetation can be predicted based on landtype; and
b. where a probable vegetation type (and thus ecotope) is mapped, the confidence level for that particular map unit is known, along with the next most probable vegetation type and its confidence level, and so on.

6.1.6 Development of a New and More Precise Terminology

The terms that are most commonly used in studies of this sort are "potential natural vegetation," "climax vegetation," and "presettlement vegetation." None of these proved useful, as the first two are based on outmoded ecological concepts and each of the three produces a theoretical result that is virtually unrelated to the present landscape. In order to discuss intelligently the progress and results of the present research, definitions were provided for three new terms: "normative vegetation" consisting of its two subsets, "actual vegetation" and "nominal vegetation." Actual occurrences are then subdivisible into primary, disturbed primary, and secondary occurrences (this last subdivision making use of well established terminology). By extension, the normative, nominal and actual vegetation can be correlated with landtypes to generate normative, nominal and actual ecotopes. The Bayesian method thus was used to predict and provide probability (confidence) levels for nominal ecotopes.

6.1.7 Indices of Estimated Depletion and Rarity

Given the new terminology and the Bayesian method, it was possible to estimate the level of depletion of any ecotope by developing a weighted average of the
proportions of its normative range in disturbed primary growth, secondary growth, and non-native growth. This method is a reliable first approximation for estimating threat in a region where levels of threat remain relatively constant over generational time.

Natural rarity was also calculated as the normalized ratio of the normative area of the ecotope type to the normative area of the ecotope type with the largest normative area. Natural rarity is a relative measure developed for each island.

Conservation priorities for individual ecotopes could then be calculated as the weighted averages of natural rarity and threat. Note that in this technique, natural rarity provides a corrective for time-related variations in the level of threat, rendering the estimate of overall conservation priority more reliable.

6.1.8 Conservation Priorities for Regions

Although the method used for the evaluation of conservation priorities for individual ecotopes is innovative, there is nothing particularly innovative about the concept. On the other hand, determining the relative conservation priorities among regions is an innovative concept, rarely applied (perhaps for political reasons). In this work, three methods were explored. These were:

a. the sum of the priorities of the individual ecotope types;

b. the mean priority of the individual ecotope types; and
c. the sum of the priorities of the individual ecotope types as adjusted by a revised skewness coefficient (another, albeit very simple, innovation of the present research).

The last method essentially adjusts the total regional priority (method a) by an index of the ratio of higher to lower priority ecotopes, thus introducing a measure of mean individual priority.

6.1.9 Network Development

In Chapter 5, a method was developed for designing a network of nature reserves that features the following characteristics:

a. all occurrences for ecotope types that are actually\(^1\) very rare are included;

b. for ecotopes that are actually moderately rare, all occurrences are included except those that involve primary agricultural land in customary tenure; and

c. for ecotopes that are not actually rare, representative segments are included such that they may serve as wide, habitat corridors in the landscape connecting and/or embedding occurrences for more rare types.

\(^1\)"Actually rare" means rare across an actual range, as opposed to normatively or nominally rare.
The first two classes were mapped using numerical methods, and the last class was mapped using a graphical solution. Finally, buffer areas were defined for network edges and streams.

Management guidelines were provided for the six generated classes of network lands; namely, core areas of undisturbed native ecotopes, core areas of disturbed native ecotopes, and buffer areas of undisturbed, disturbed, and secondary native ecotopes and also of non-native ecosystems. Ecosystem restoration goals were assigned to the classes containing other than undisturbed native ecosystems.

6.1.10 Characterization of the Network

Perhaps the most frustrating aspect of the present research was the attempt to find quantitative methods for characterizing the resultant conservation networks. Area, perimeter, and shape were straightforward. Idrisi provided internal modules for the determination of the first two. Roundness and fractal indices from the literature were used for shape (although the roundness index required inversion from its normal form), and a common diversity index was used for relative diversity measures. The remaining attempts to characterize network permeability, connectivity, circuitry, etc. using existing indices proved to be mostly fruitless.

The Shannon-Weaver index of diversity was calculated for the networks, the normative landscapes, and the actual landscapes of each island. The diversity of the
networks relative to the normative landscapes were moderately high, and the diversity of the networks relative to the actual landscapes were very high. Normative and actual relative diversities provide good measures of a network’s success at capturing the information content of the normative and actual landscapes. The lower the separation between diversity indices for normative and actual landscapes and the higher the relative diversities of the network in each case provide good measures of the probable success of the network with the conservation of diversity.

It was desirable to develop some measure of the contiguity and distribution of the networks relative to their contextual landscapes. This provided the toughest challenge of the characterization task. Both networks were determined to be highly autocorrelated, an indication, in this case, of success. After exploring the available indices of connectivity and network circuitry, entirely without success, a new index of extension was devised. This was defined as the normalized ratio of the mean distance of the average point on the island to the nearest extension of the network core to the mean distance of the average point on the island from the centroid of the island. The index of extension provides a very handy and reliable method for determining the extent to which a network permeates a landscape. Combining information from this index with that from roundness and fractal indices, one can explain extension with reference to the levels of boundary convolution and network fragmentation. If both of the latter are relatively low, then a high index of extension is a measure of successful, representative network generation.
6.1.11 The Relative Influences of Size, Shape, and Culture

Contrary to expectations, no deterministic relationship could be found that related the shape of the networks directly to the size or shape of the islands. In every case, the mechanisms whereby island size and shape influenced the networks were themselves translated by the influences of human interactions with the environment. For these reasons, generalization of the networks themselves beyond populated, tropical, forested islands (except makatea islands) seems unsound. On the other hand, all indications are that the process of network generation can be generalized and applied in other kinds of landscapes. Ultimately then, the most significant innovation of the current research is the generation of the methodology, REAL Conservation, as outlined in Chapter 5.

6.2 Evaluation of Success

6.2.1 Verification

The verification of a model is the determination that the model accurately represents the assumptions on which it was built, i.e., that it behaves the way it was designed to behave (Jeffers, 1978, Kitching 1983). For example, given the assumptions in Chapters 1 and 2, a nature reserves network model for 'Upolu in Western Samoa should:

a. include a selected set of spatial relationships that parsimoniously but effectively reflect the spatial relationships among the normative ecotopes of 'Upolu;
b. include viable examples of all of 'Upolu’s ecotopes, placing highest priority on those that are rarest and most threatened, and exhibit high capacity to contribute to the recovery of rare and threatened ecotopes; and
c. include an optimally small portion of prime agricultural lands in customary tenure, and make a significant contribution to soil and water conservation.

Verification is almost tautological, but it is an important step. It is analogous to measuring a board after it has been cut to determine if the final product meets the specification in the plan. Certain steps can be taken to increase the likelihood of the model’s successful verification (to assure that the board was cut accurately to length):

a. Modelling tools should be selected carefully and their application must be thoughtful so that the different tools are synergistic and so that errors do not multiply. The process of model development must be informed by the best available theoretical and experimental literature;
b. The model should be based on the best possible original data, so that weaknesses in the data do not contribute to failures in the model; and
c. The model’s internal consistency should be rigorously evaluated by comparing the final product with original premises.
Chapters 1 and 2 provide a review of the scientific background and consequent principles for the conservation of ecologically stable (or metastable) landscapes. The following sections briefly restate the most significant principles and discuss their influences on the final methodology and the models it generated.

6.2.1.1 Biological Diversity

Original Premise: Biological diversity in a region includes genes, taxa, populations, ecotopes, landscapes, and the patterns generated by ecological events. Together, these comprise the information content of the ecological region.

REAL Conservation and the Samoan networks quite clearly capture ecotopes, and by extension, landscapes very efficiently. Ecological patterns are captured efficiently only at the scale of the networks themselves, i.e., the spatial relations among ecotopes. At smaller scales, these patterns are highly variable over space and time, and the comprehensiveness of their conservation is exactly synonymous with the comprehensiveness of the spatial coverage of the landscape by the networks (roughly 40% for both islands, counting buffers).

Genes, taxa, and populations are more problematic. If taxa are well represented by populations in or extending across ecotopes, then it is very likely that most taxa are captured by the method, even though no population occurrence data were used. For rare taxa, this is not a safe assumption! The individual populations
outside the networks, and thus the genetic variability they may represent, by
definition are not captured by the method. It is therefore essential that the REAL
Conservation method be supplemented by adding rare and threatened species
populations to the original data base, that these taxa and their populations be ranked
according to conservation priority, and that the populations be incorporated into the
network design phase. Fortunately, the methodology for this process is already well
established by The Nature Conservancy, and can be incorporated essentially without
modification (the Natural Heritage Inventory methodology; Jenkins 1977, 1981,
1982, 1985, 1988). In other words, the REAL Conservation methodology efficiently
captures beta and gamma diversity, but the Natural Heritage Methodology is required
to capture alpha diversity at the level of the landscape. Thus, the interdependence of
ecosystem and species conservation approaches is illustrated.

6.2.1.2 Ecosystems

Original Premise: Ecosystems are not arbitrary subsets of the environment.
Each ecosystem is a locus of most probably element interactions suspended within the
context of a larger ecosystem.

The present research is based on the assumption that ecosystems cannot be
arbitrarily defined. Thus, ecosystems are defined as the unique intersections of
vegetation and landtypes at the scale of the stand or ecotope. This approach holds
true for the individual ecotopes to the extent that landtype is ecologically
deterministic, a premise well supported in the literature. It also holds true for the total landscape, but only if the Theory of Landscape Ecology holds true. There is much evidence supporting the former assumption. The latter is an unproven theory that seems intuitively true and that is often assumed to be true (as in the present research) because the mechanisms of ecosystem interactions are so clearly shaped and channeled by the configuration of the landscape. It is stated here, for the first time, as a theory to be disproved if possible.

6.2.1.3 Succession, Climax, and the Patch Dynamic

**Original Premise:** The concepts of succession and climax are no longer very useful in their traditional forms because the spatial and temporal scales of the ecologist are more flexible than either concept traditionally supports. A much more useful concept is that of the patch dynamic.

The REAL Conservation methodology does not include the kind of long term research that would be necessary to gauge the patch dynamics (that is, the characteristic size, shape, persistence, micro-climate, and internal succession and composition of ecosystem patches) of a landscape. The assumption is made, again on the basis of the Theory of Landscape Ecology, that the landscape as a whole is the product of its patch dynamic (by definition), and therefore, capturing a parsimonious and compositionally and spatially representative subset of the landscape will capture
the patch dynamic at some level. The patch dynamic of the landscape is conserved, but the patch dynamics of the individual ecotopes may not be.

6.2.1.4 Ecotones, Edges, and the Boundary Model

Original Premise: Ecotones and edges are significant moderators of ecosystem interactions, especially in the special case of interactions among native and non-native ecosystems. According to the boundary model of Schonewald-Cox and Bayless (1986) these elements should be deterministic in the design of nature reserves.

A parsimonious set of ecotopes, selected to retain perfectly their spatial relationships will, by definition, capture and conserve the ecotones extant in the actual landscape. Unfortunately in Samoa, the ecotones that probably once existed between coastal ecotopes are largely lost, and their conservation is now impossible. The buffers designed for the networks were sized at a minimum of 300 m in width to absorb edge effects.

The effort to provide buffers for the most isolated and rarest ecotope types resulted in the largest fraction of buffer area being generated on non-native ecotope lands. These buffers cannot absorb edge effects, and in fact will contribute edge effects, until they are restored to native or pseudo-native status. A successful effort was made to minimize convolution of the non-stream buffer boundaries, thus
minimizing the various edge effects that can be exacerbated by an interdigitated boundary.

6.2.1.5 Hierarchies

**Original Premise:** Ecosystems exist in hierarchies, and this hierarchical nature results in constraints on the ways ecosystems can be classified and on the ways that analyses can be conducted.

The vegetation and ecotopes of Western Samoa were classified in hierarchical structures. The type and entity rules of hierarchical classification were observed carefully. The resulting classifications thus can be subjected to taxonomic management as new information becomes available. The model development was done entirely at one hierarchical level (that of the ecotope) and scale inconsistencies and changes were carefully avoided.

6.2.1.6 Stability

**Original Premise:** A steady-state system is one where the system’s level of complexity is maintained in spite of perturbations. Stability is the tendency of an ecosystem to maintain itself in a steady-state condition. Meta-stability is the tendency of an ecosystem to exist within a domain of multiple steady-state conditions. Measures of stability at one hierarchical level cannot be used to make inferences about stability at another level.
Given the nature of an island’s ecology, its landscapes are much more likely to be meta-stable or not stable, than simply stable. Thus, the long-term conservation of island landscapes cannot be based on some measure of stability and its component causes. This entire exercise was premised on the assumption that a stable landscape can be conserved by conserving the diversity of its component pieces (ecotopes) without any assumptions about the local stability of any given ecotope or the local patch dynamic.

Unfortunately, the rarity of ecotopes attributable to threat and, in some cases, exacerbated by natural rarity, leads to a very poor prognosis for survival of small fragments in a meta-stable or unstable environment. The model is weakest in its application to the conservation of rare ecotopes existing in small, isolated fragments. In this respect, it exactly reflects ecological reality.

6.2.1.7 The Equilibrium Theory of Island Biogeography

**Original Premise:** The Equilibrium Theory of Island Biogeography states that the number of species on an island will vary directly with its area and inversely with its isolation. Various authors have extended this concept to habitat "islands," and subsequently to nature preserves as special cases of the latter.

Although support for the conservation corollary of this theory is weak, there is experimental evidence supporting the notions that nature reserves should be as large
as possible and as little isolated from each other as possible (barring genetic reasons for separating or splitting populations). The REAL Conservation methodology is quite faithful to these principles. Unfortunately, the prior fragmentation of the landscape provides a severe complication.

6.2.1.8 Cartographic Models

Original Premise: A model is a gray-box system that simulates a more complex system where the internal processes of responding to inputs to generate outputs are only partially understood. A model, in effect, facilitates an understanding of the behavior of a complex system by simplification. A cartographic model is a structural and sometimes analytical model based on the spatial relations among fields and objects (points, lines, and areas) representing the surface of the earth.

This research includes an implementation of a cartographic modelling approach to the design of a nature reserves network. The model is implemented on a geographic information system. The basic units of the modelling process were the digital elevation model; vector files for road, streams, and coast data; and various thematic coverages of data including vegetation, geology, prime agricultural land, and land tenure. Intermediate or synthetic variables included slope, aspect, elevation, landtype, and ecotope. Many of the tools available in map algebra were used along the way.
6.2.1.9 Error in Spatial Data

Original Premise: Error in cartographic models results generally from two sources: the ability to freely change scales, and the ability to overlay multiple, imperfect data sets.

In the present research, scales simply were not changed. All research and development was done at the same scale and resolution in the GIS once the original data were loaded. Input data were carefully selected to be of similar scales (e.g., this was a reason for using geological rather than soils data).

On the other hand, there was quite a bit of variability in the quality of the input data, and only in the case of vegetation data, was the reliability of the data fully known and mapped. To avoid increasing error, most constructions and analyses involved only one or two data layers. The notable exception was the generation of landtypes, wherein four distinct data layers were used. Three of these were developed from an interpolated digital elevation model based on fairly coarse but probably accurate, recently collected and verified topographic data. The landtype data must be considered to be fairly fuzzy.

Slivers in the GIS data are likely to be artifacts of this fuzziness. For that reason, slivers below a certain size were discarded in the modelling process, creating the small but real possibility that very rare ecotopes were discarded from the model at
the same time. For these reasons, the ecotope maps must be confirmed in the field as conservation is implemented.

6.2.1.10 Ecologically Stable Landscapes and Species

Original Premise: An ecologically stable landscape will not lose species through extirpation or extinction at faster than normal rates. In order to sustain a species, the landscape must sustain its minimum viable population, that is, enough actively reproducing adults to keep inbreeding below about 1% per generation and to prevent the loss of heterosis through genetic drift. The rule-of-thumb for vertebrates is an effective population of 500 actively reproducing adults.

Although the networks and the methodology developed do not deal with species explicitly, they should provide adequate conservation for most species by the inclusion of habitats in the ecotopes of the landscape. A useful test of this premise would be to determine if the networks can sustain, in the absence of extraneous factors such as over-hunting, minimum viable populations (MVP) of a wide-ranging and threatened species.

The Samoan flying fox (Pteropus samoensis) is such a species. It is also generally recognized as a "strong interactor" or "keystone species," the extinction of which would result in the extinction of many other, dependent species for which it is the primary pollinator and seed disperser (Cox et al. 1991, Fujita and Tuttle 1991;
also see Fleming 1988 for supporting information based on studies of other flying foxes or fruit bats). Unfortunately, the species is threatened by excessive hunting and habitat loss (Engbring 1989).

*Pteropus samoensis* uses forage and roosting all of the native forest ecotopes found in Samoa, but the preference is for well-developed or mature, Lowland and Montane Rain Forests. Although the species will forage in agroforests, it prefers native forests (Engbring 1989).

During 24 30-minute counts taken over 10 days in good habitat, Engbring (1989) counted *P. samoensis* on both islands. Engbring estimated that the population density of *P. samoensis* was 1.92 individuals per km$^2$ in good habitat (Lowland or Montane Rainforest) in Western Samoa. Given a normative habitat for this species of nearly 3,000 km$^2$, we could expect a total population of nearly 6,000 individuals or an effective population of roughly 3,000 (holding current hunting pressure constant, and using a very rough estimate of 50% for effective membership in a population). The actual habitat measured in this research was 1344 km$^2$ capable of supporting an effective population of approximately 1350 individuals. The conservation networks include 868 km$^2$ of good habitat and can, therefore, support a metapopulation of about 810 individuals with an effective population of roughly 405. Given the roughness of the estimate for effective membership, we can speculate that the proposed conservation networks may, between them, support an MVP for *P. samoensis* at 20%
lower than the 50/500 rule-of-thumb. But this is extremely inconclusive! Note also that these calculations are based on the assumption that hunting pressure is held constant. If hunting pressure is relieved, then population densities in suitable habitat can be expected to go up.

6.2.1.11 Corridors

Original Premise: Corridors are a useful strategy for combating fragmentation and its deleterious effects in the landscape. However, corridors, to be useful and not dangerous, must be of high quality habitat and at least wide enough to sustain an interior space free of edge effects.

This principle was followed scrupulously in the development of the networks and the methodology. The result is that corridors are used in some places in the network, especially as part of the graphical solution incorporating more common ecotopes, but corridors cannot be used in conjunction with the smallest and most isolated ecotope occurrences.

6.2.2 Validation

Validity is the extent to which a model produces results that correctly and accurately reflect the real world, that is, what really happens. A model is considered valid (true) if its outputs successfully mimic the real world within established accuracy goals. Data that are used experimentally to test validity must be completely
independent of the data used for model development. The normal process for model validation is to determine empirically the model's predictive capacity (Caswell 1976, Hall and Day 1977, Jeffers 1978, Kitching 1983, Lancia et al. 1982, Mankin et al. 1975, Marcot et al. 1983, van Horne 1983). To use an analogy, a standard table of loads, beam sizes, and spans is a useful model employed by architects. The table is based on past experience (data) plus some assumptions about material quality and margins of error (estimations of risk). To validate the model, various beams must be tested with various loads until the statistical evidence of beam successes and failures either supports or forces the revision of the model. This may be a lengthy process, as some beams that will fail may not do so for many years.

Unfortunately, the validity of geographic and ecological models is much more difficult to determine. Temporal and geographic scales are prohibitive for much experimental research. Furthermore, rare ecotopes cannot be placed at risk to serve as unconserved controls in any such experiments.

In a discussion of validation, Mankin et al. (1975) distinguished between descriptive and predictive validity as subsets of the validation question. Descriptive validity is the proportion of the system that is accurately or truthfully modeled. It is always, by definition, reduced by symbolic representation. Predictive validity is the portion of the model's output that is correct. In a cartographic, and therefore structural model, descriptive validity can be quite high, depending on the quality of
the input data and the skills of the cartographer-modeler. Predictive validity is another matter.

Another way of illustrating the contrast of predictive and descriptive validity is to consider Newton’s Theory of Gravitation as a model. The theory is not descriptively valid in that it does not truthfully model any part of a real system. Einstein taught us that gravity is an entirely different phenomenon than that which Newton visualized. On the other hand, Newton’s Theory is highly predictively valid, correctly predicting the behavior of nearly all solids in nearly all circumstances.

In the present research, the question of descriptive validity can be addressed by the question, "do the REAL Conservation methodology and its resultant networks sufficiently account for all the variables that they should?" Alone, they clearly do not. On the other hand, taken in tandem with data on threatened and rare taxa, they appear to be adequate. Is the model descriptively valid? Within the constraints of data precision and accuracy, the model appears to be highly descriptively valid, with the possible exception of tiny, real ecotopes dropped as slivers, and slightly larger slivers perhaps erroneously retained as rare ecotopes. Is the model predictively valid? We may never know.

Consider a simple species conservation model based on the use of minimum viable populations to avoid inbreeding depression and the loss of heterosis (Frankel
and Soulé 1981; Schonewald-Cox et al. 1983; Soulé 1986a, 1987; Soulé and Wilcox 1980). More than 50 generations of the average rare species could be required to determine whether the plan will fail for that species for genetic reasons (based on computer simulation by Boecklen 1986). Even then, it might take that species many more generations to actually become extinct. Determination that the extinction was attributable to failure of the model probably would be impossible.

In the case of an ecosystem conservation model, the problem is more difficult. Assume that the Government of Western Samoa makes no changes in the final conservation plan based on the models developed here. Assume also that the Government immediately and completely implements the plan and maintains that implementation for many, many years (essentially forever, since we have no predictive tools for the timing of ecosystem collapse). The models predict that few ecotopes will be lost (collapsed or extirpated) in Western Samoa due to failure of ecosystem interactions. No predictions are made about other stochastic causes for the possible collapse or extirpation of ecotopes. When taxa or ecotopes do collapse or disappear it will be very difficult to identify causes. If no ecotopes collapse or disappear, it will not be possible to conclude that the landscape conservation plan is responsible. In other words, a protected areas system based on a model cannot be used experimentally to validate (corroborate) the model’s predictive reliability.
Although REAL Conservation is a methodology, its products are analytical models that cartographically present conservation solutions given limiting parameters. On the other hand, the networks potentially can also be treated as simulation models.

Simulation is often the only alternative for determining the predictive reliability of an ecological model, and several authors have written about it (Fahrig 1991, Merriam et al. 1991, Robertson et al. 1991, Sklar and Costanza 1991). The most common form of simulation is to develop a set of difference equations that characteristically are not easily subject to simultaneous solution. Then, given a starting point or base state for the system, iteration of the equations simulates the behavior of the larger system. Today, virtually all simulation is done on computers, because these devices are very well suited to performing iterative tasks with many, many repetitions.

Sklar and Costanza (1991) describe how a simulation model might be formulated for a process-based landscape model. In such a case, algorithms would be defined describing the flows of materials and organisms between ecotopes in the landscape (a very significant research need). Assuming such algorithms could be developed, and assuming critical limits for ecotope stability or meta-stability could be defined for these flows, then a process-based landscape model could be developed and simulated.
Merriam et al. (1991) describe several possible spatial configurations for such a model based on flows (corridor, non-corridor, pool, pool/corridor hybrid, sequential habitat, and three dimensional mosaic). Each of these is essentially a single species or guild approach. A successful simulation for the conservation networks would undoubtedly involve the development of a meta-model composed of single species or guild models (also see Fahrig 1991).

Models of these sorts would be extremely helpful in theoretically (not operationally!) validating the network outputs of the REAL Conservation methodology. The missing pieces are difference equations with critical limits identified describing inter-ecotope flows of materials and organisms.

6.2.3 Summary of Success

A brief outline provides a useful summary of the measures of success discussed above:

I. Verification is based on conformance original assumptions, with high levels of conformance generally indicated.

II. Validation (What is the truth?)

A. Descriptive Validity - Within the constraints of spatial accuracy and precision, the model is descriptively valid.

B. Predictive Validity
1. **Theoretical determination** - possible by simulation if complete sets of difference equations can be developed for inter-ecotope flows of materials and organisms (unlikely)

2. **Operational (experimental) determination** (impossible)

### 6.3 Conclusions

The theory of landscape ecology is the text within which one finds the foundations of the spatial analyses of landscape ecology. Many hypotheses have been grounded in this text, and many of the references cited for it above document explorations and/or attempted tests of such hypotheses. The tests have been positive, and in the language of Popperian positivism, the theory is reasonably well corroborated.

The current research was not a traditional example of hypothesis development and testing in the context of the theory of landscape ecology. It was not intended to test any hypothesis about spatial determinism in ecosystem interactions at the scale of the landscape. It was not, thus, a strictly positivist exercise (Hill 1981). Instead, this research was an investigation into the possibility of the development and application of several closely related, sometimes novel methodologies, together comprising a complex model for ecosystem-level conservation at the scale of the landscape, given the foundation theory.
Is REAL Conservation a useful methodology? Does it produce networks for landscape conservation that conform well with the best theoretical thinking and experimental results in the disciplines? The answer to both questions is a qualified "yes." The methodology is straightforward and useful, and its various steps are easily understood and replicated. On the other hand, as developed herein, it is missing a rare species component, and this must be factored in if the methodology is to be really useful.

Close analysis of both process and products indicates a model that is strongly verified against all original premises except that of minimum viable populations for threatened and widely ranging species as tested against the single case of *Pteropus samoensis*. In this case, the model is weakly verified by the results of a crude analysis of MVP for the flying fox. The model is also descriptively valid with the addition of a rare species component.

Finally, although the model cannot be experimentally determined to be operationally, predictively valid, it can be tested by simulation to determine if it is theoretically, predictively valid. The Theory of Landscape Ecology provides the exact list of requirements for such a simulation. It is daunting! One must know at least approximately the nature, the consequences, and the critical thresholds of inter-ecotope processes in order to generate the simulation.
It is doubtful that any other methodology presently exists that will systematically, efficiently, and parsimoniously capture ecosystemic diversity for conservation as well as the proposed REAL Conservation methodology. The methodology is well grounded in modern ecological concepts and the principles of Landscape Ecology and Conservation Biology. Its step-wise approach is defensible and replicable. The networks that it generates as models for conservation should, if closely followed, do much to enhance the likelihood of the persistence of ecologically stable landscapes.
APPENDIX A

INSTITUTIONAL SUPPORT

A.1 Backgrounds on the Institutions Providing Support for Projects Contributing to this Dissertation

A.1.1 The Biological Diversity Support Program (BDSP)

On 31 May 1988, the chief executive officers of the International Institute for Environment and Development -- US (now merged with the World Resources Institute), The Nature Conservancy (TNC), and the World Wildlife Fund-US (WWF-US) signed a memorandum of understanding to establish a joint venture to inform and focus the biological diversity programs of the United States Agency for International Development (USAID) and to provide a sound scientific basis for USAID biological diversity investments. The memorandum created a joint venture, now referred to as the Biological Diversity Support Program (BDSP). WWF-US is named as the lead agency in a ten year contract with USAID signed on 9 June 1988. Under the terms of this contract, WWF-US and the parties in the joint venture agree to provide USAID with technical assistance, to establish a small matching grants program for biological diversity research, to establish a training program for client country representatives in proposal writing and research development, to establish an information and evaluation network, and to conduct pilot demonstrations. These last are specifically to include pilot projects adapting the TNC Conservation Data Center model (see TNC below) for application in less developed countries.
A.1.2 The East-West Center Environment and Policy Institute (EAPI)

The East-West Center, Environment and Policy Institute\(^1\) has a long-standing interest in biological diversity within its Land, Air and Water Management Program. Under this program, a specific project in Biological Diversity and Protected Areas was initiated in 1986. Examples of EAPI Pacific island biological diversity activities include, in addition to those discussed below, a six-week workshop on managing biological diversity in parks and protected areas during the summer of 1987, development of a management plan and assistance with financial support for the Fiji Crested Iguana reserve, and establishment of the MacArthur Foundation Pacific Islands Initiative.

A.1.3 The South Pacific Regional Environment Programme (SPREP)

The South Pacific Regional Environment Programme is the technical coordinating environmental agency for 22 countries and territories of the tropical Pacific. One of SPREP's primary missions is to conserve the biological diversity of the SPREP region. Since 1980, SPREP has been actively involved in the planning and establishment of nature and natural resources reserves, in environmental assessment, in environmental education, and in providing technical assistance with the promulgation of regional and national policies designed to conserve biological diversity and natural resources in the context of sustainable development. The SPREP

\(^1\)The Environment and Policy Institute is now dissolved, and its component parts partly incorporated into an East-West Center Environment Project (May 1993).
secretariat attempts to respond to country requests for various kinds of conservation and environmental protection assistance within the context of a regional overview of needs and opportunities (Pearsall 1990a). The Fourth South Pacific Conference on Nature Conservation and Protected Areas (Port Vila, Vanuatu, 4-12 September 1989) prepared an Action Strategy for Nature Conservation in the South Pacific Region outlining in some detail SPREP’s goals and objectives in biological conservation for the coming years and containing country specific project needs (SPREP and IUCN 1989).

A.1.4 The Nature Conservancy (TNC)

The Nature Conservancy is a private, not-for-profit, international corporation dedicated to the conservation of ecologically significant areas and the biological diversity they support. TNC works by identifying significant areas and insuring their protection through outright acquisition and management (exclusively in the US) or through assistance to government and other conservation organizations (in the US and internationally). An essential component of the TNC strategy is the Conservation Data Center (CDC). A CDC is an institutionalized, staffed and equipped, dynamic atlas of the locations of the most significant elements of biological diversity in a region or country. These may be rare plants, animals, ecosystems, and habitats. The atlas itself is typically computerized, but it is complemented by a set of paper maps and both computerized and paper versions of supporting data (Jenkins 1977, 1985, 1988; Master 1991).
A.1.5 The United States Agency for International Development

The primary mission of the United States Agency for International Development is to promote sustainable development in those countries determined to be eligible for US foreign assistance and where basic human needs are not being met. An ancillary but closely related mission of the agency is to insure that this development produces the least environmental damage and, in the ideal case, includes provisions for conservation of biological diversity (USAID 1985). USAID's South Pacific Regional Development Office (USAID/RDO/SP) is actively involved with the conservation of biological and ecological diversity (USAID/RDO/SP 1988, Pearsall 1988).

A.1.6 The United States Fish and Wildlife Service (USFWS)

The United States Fish and Wildlife Service is the operational arm of the United States Government that is concerned with preserving and enhancing populations of and habitats for the native wildlife (including both plant and animal species) of the US and its territories and affiliated countries. USFWS programs include, among others, the conservation of threatened and endangered and other important (e.g. game) species, modelling habitats for selected species, environmental education, various approaches to habitat enhancement and conservation, and habitat restoration and loss-mitigation.
A.2 The Project for Vegetation Mapping in Western Samoa: EAPI, IFREMER, and SPREP

Beginning in 1987, discussions were held between SPREP and the East-West Center Environment and Policy Institute on the possibility of conducting an inventory of terrestrial vegetation in Western Samoa leading toward revision of the existing national parks and protected areas plan (Holloway and Floyd 1975). SPREP had been requested to support the project by the Government of Western Samoa in 1986. The goal was to develop a new plan for a system of protected nature reserves in the country. By October 1988, agreement had been reached, and Pearsall began the project officially on the first of January 1989 under the auspices of EAPI, with Dr. Lawrence Hamilton, Senior Research Associate, overseeing the management of the project at EAPI and Mr. Peter Thomas, Protected Areas Officer, as project manager at SPREP.

The EAPI/SPREP project provided for a definition of the main terrestrial vegetation types for Western Samoa, a set of maps at 1:20,000 showing the mappable units of native vegetation, and revision of the 1975 national parks and protected areas plan to form a new proposal for a national system of reserves that would include viable, representative examples of all of Western Samoa's terrestrial vegetation.

Dr. Lionel Loubersac of the Institut français de recherche pour l'exploitation de la mer (IFREMER) agreed to provide the EAPI/SPREP project with a SPOT satellite image for the western two thirds of the island of Savai'i. He also agreed to
provide training for its use. During January 1990, Pearsall, Loubersac, and other personnel from the Station polynésienne de télédétection in Papeete, Tahiti, French Polynesia (the Station) prepared contrast enhanced SPOT satellite images of the western two thirds of the island of Savai'i. These were used to revise the EAPI/SPREP products.

A.3 Building Ecosystem Data for a Western Samoa CDC: TNC and BDSP

In January 1988, TNC entered into an agreement with USAID to evaluate the possibility of building a CDC program in the South Pacific Region and contracted with Pearsall for the work. This project was successful (Pearsall 1992), and in October 1989, TNC and the BDSP established a two year project to demonstrate the utility of CDCs in the South Pacific. The first component of that project was to establish a pilot CDC in Western Samoa using the ecosystem data gathered during the EAPI/IFREMER/SPREP project.

A.4 Criteria for Ecosystem Classification and Conservation in the Pacific: USAID/RDO/SP, BDSP, EAPI, SPREP, TNC, and USFWS

In 1990, USAID/RDO/SP organized a group of agencies and institutions to work on the task of developing a hierarchical classification and conservation criteria for the ecosystems of the tropical insular Pacific. These included BDSP, EAPI, SPREP, TNC, and USFWS.
An Expert Workshop on Ecosystem Classification and Conservation Criteria for the Tropical Insular Pacific was held at EAPI in Honolulu, Hawaii, 11-15 March 1991. The workshop was sponsored by the group of institutions listed above, and co-convened on behalf of those agencies by Lawrence Hamilton, Paul Holthus, Jim Maragos, Peter Thomas, and myself. Two background papers were prepared for that meeting (Fosberg and Pearsall in press, Maragos 1991a).

At the workshop, three working groups were established. These addressed the tasks of classifying and establishing conservation criteria for terrestrial, marine, and freshwater ecosystems. The work of these three groups was compiled in four papers (Maragos 1991b; Pearsall 1991a, 1991b; Polhemus in press), circulated to all the original workshop attenders and other experts, and presented in the Symposium on Ecosystems Classification for the Tropical Insular Pacific, XVII Pacific Science Congress (28 May 1991, Honolulu, HI).

Based on input from that symposium, Pearsall contracted with TNC to compile a final paper for circulation and review. This paper was distributed in October 1991 (Pearsall 1991c).

A.5 Graduate Studies: EAPI and University of Hawaii

All three of the projects listed above were intended to provide most of the basic data for this doctoral dissertation. To further this end, the United States
National Science Foundation provided an additional grant via the UH Social Science Research Institute to support the project. The principal investigator of record for that grant was Dr. Brian Murton, Chair of the University of Hawaii Geography Department, and chair of Pearsall’s graduate committee. The UH Geography Department provided Pearsall with an office, access to various equipment and expertise, and assistance with some office expenses during all three of the projects discussed above.

Basic salary support during the first two thirds of the EAPI/IFREMER/SPREP project was provided by EAPI through a graduate student fellowship, again under the supervision of Dr. Hamilton. EAPI also provided a field studies grant to support travel and expenses associated with Pearsall's visit to the Station in Papeete.
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