

PATCH DYNAMICS AND THE DESIGN OF NATURE RESERVES

S. T. A. PICKETT†

Plant Ecology Laboratory, Department of Botany, 289 Morrill Hall, University of Illinois, Urbana, Illinois 61801, USA

JOHN N. THOMPSON

Ecology Program, 320 Morrill Hall, University of Illinois, Urbana, Illinois 61801, USA

ABSTRACT

Island biogeographic theory has been applied to the design of nature reserves. However, immigration, which is important in maintaining species equilibrium on true islands, will not contribute significantly to the maintenance of equilibrium on reserves in the future because of the disappearance of recolonisation sources. Consequently, extinction becomes the dominant population process, and the internal disturbance dynamics become the critical design feature of reserves. The design of reserves should be based on 'minimum dynamic area', the smallest area with a natural disturbance regime which maintains internal recolonisation sources and hence minimises extinctions. Determination of minimum dynamic area must be based on knowledge of disturbance-generated patch size, frequency, and longevity, and the mobilities of the preserved species. These features have not all been explicitly considered in the previous island biogeographic design recommendations.

INTRODUCTION

Nature reserves are habitat islands. They are areas of natural landscape surrounded by expanses of culturally modified habitat. Because of this, the theory of island biogeography has been applied to the design of nature reserves (see review by Diamond & May, 1976). The degree of isolation from sources of colonisers determines the rate of immigration, while the island area determines the population sizes and thus the rate of extinction. The immigration and extinction rates together determine the number of species that will inhabit the island at equilibrium (MacArthur & Wilson, 1967). The purpose of this paper is to stress the importance

† *Present address:* Department of Botany, Rutgers University, New Brunswick, New Jersey 08903, USA.

of the internal dynamics of habitats in the design of reserves as colonisation sources become increasingly less available.

COMPONENTS OF EQUILIBRIUM

The components of equilibrium on both true and habitat islands are the same, but the relative importance of these differs between the two types of system. True islands, even very isolated ones, have very large continental species pools from which colonisers are drawn. The island characteristic which largely determines the magnitude of the flux of colonisers is distance from the source. More distant islands will receive fewer colonists. The second island character important in determining its equilibrium species number is area. Increased area permits large population sizes and thereby reduces the probability of extinction. Thus, larger islands have lower extinction rates. The number of species that an island will support at equilibrium is that number where extinction equals immigration. Most true islands will approach equilibrium from below (Wilson, 1969). The only non-island character important in determining equilibrium is the continued existence of the species pool supplying colonists.

Nature reserves as habitat islands are influenced by the same components: the island characters of area and isolation, and the population processes of immigration and extinction. However, for reserves the rich, extensive source areas do not, or will not, continue to exist (Meijer, 1973; Diamond, 1976; Terborgh, 1976). The reserves themselves must perform most if not all of this function as increasingly more land in all biomes is developed or disrupted. Because of this, the immigration rate, which is so important in maintaining equilibrium on true islands, is likely to decline significantly (Terborgh, 1974a; Willis, 1974; Diamond, 1976). Extinction will then become the dominant population process affecting equilibrium in reserves and species numbers will decline to a new level. There will still be immigrants, but such species will be the widespread, fugitive types which do not need reserves for their survival (Willis, 1974; Terborgh, 1976; Whitcomb *et al.*, 1976). Species requiring continuous habitat (Peterken, 1974) or specialised habitat types (Geist, 1971) for their survival or dispersal will not be able to disperse to sites where they have become extinct (Terborgh, 1974b).

The equilibrium process on habitat islands will somewhat mimic that on land bridge islands where species number is determined by extinction. These land bridge islands, isolated since the end of the Pleistocene, have more species than oceanic islands of similar area and isolation (Diamond, 1972), but have fewer species than the continental areas with which they were once continuous. Their species numbers are decreasing, or relaxing, to new lower equilibria, due to the current dominance of extinction over immigration (Diamond, 1972; Willis, 1974). It is the first species characteristic of closed, undisrupted habitats to become extinct.

Because extinction is the dominant process in ecological time on land bridge and newly-created habitat islands, the factors influencing it deserve closer examination. As for true islands, area affects extinction, with smaller areas increasing the probability of extinction due principally to reduced population sizes (Simberloff, 1974; Terborgh, 1974a; Elton, 1975). Small populations are particularly subject to fluctuations and random events. However, in addition, small populations, or populations necessarily confined to small areas, will be more subject to extinction due to the internal dynamics of the island landscape.

PATCH DYNAMICS

Internal dynamics are generated by patterns of disturbance and subsequent patterns of succession, and may be called patch dynamics. Three sets of phenomena and processes define the dynamics of patches on a landscape scale. The disturbance regime determines the size, density and temporal frequency of patches. The internal structure of patches is determined by species composition, population densities, population dispersions and organism geometry. As a result of their internal features, patches will have characteristic longevities. Many attributes of patches have been considered by Levin (1976) for the landscape scale, and by Root (1975) and Thompson (in press) for the within-community scale.

On continental landscapes, patch dynamics are complex and of profound importance. Patches are generated by many agents whose direct effect is on vegetation, for example, fire, which is one of the most common. It is important, for example in temperate deciduous forest (Loucks, 1970), boreal and montane coniferous forest (Heinselman, 1971; Wright, 1974), grassland (Old, 1969), chaparral (Vogl & Schorr, 1972), and tropical deciduous forest (Walter, 1971). Winds and windstorms are important disturbance agents in deciduous forest (Jones, 1945; Lindsay, 1972; Wright, 1974), coniferous forest (Sprugel, 1976) and the tropics (Webb, 1958). Ice and snow (Siccama *et al.*, 1976), floods and landslides are important in some systems (Hack & Goodlett, 1960). Biotic factors also contribute to the disturbance regime. Natural death of old individuals is an important gap generator in all systems (Bray, 1956; Forcier, 1975). Disease and herbivory (Mattson & Addy, 1975) are also very common. Animals disturb some systems (Bratton, 1975; Platt, 1975). The contribution of these various agents to the disturbance regime and hence patch dynamics depends on the climate, topography and biota of the site. Disturbance may occur on scales ranging from the removal of one individual (Horn, 1976) to the opening of many km² (Wright, 1974) as a result of different disturbance agents or the change in severity of one type.

Disturbance and succession are ubiquitous landscape features. As a result, the natural landscape is a mosaic of successional patches of various sizes (Whittaker, 1953) whose diversity depends partially on patch dynamics (Loucks, 1970) and

which provides opportunities for evolutionary divergence of species (Pickett, 1976). Even climax species must have a fugitive aspect (Harper, 1965) to exploit gap disturbance in the mature community (Jones, 1945; Forcier, 1975). Preservation of landscapes must allow for the continued operation of these processes (Stone, 1965; Houston, 1971; Wright, 1974; McLean, 1976).

Patch dynamics must occur with equal importance on true islands. As a mechanism for causing local extinction of species they are an unfactored component of the species-area relation. Disturbance of a given size and frequency is much more likely to cause extinction on a small island by reducing population sizes below threshold levels. Patch dynamics have remained unfactored because the comparative and empirical approach to island biogeography could rely on area to predict equilibrium species number, and because of the importance of the immigration component on true islands. Processes which we would identify as patch dynamics have been recognised by students of oceanic island biogeography (Willis, 1974; Diamond, 1975*b*, 1976; Wilson & Willis, 1975). The predictive role of patch dynamics in species equilibria will increase from oceanic through land bridge to habitat islands because of the increased importance of extinction and consequent relaxation.

The use of patch dynamics in the design of nature reserves then requires knowledge of the disturbance regime and the associated patterns of succession. The type of disturbance will influence all other patch characteristics. Thus disturbance type is fundamental background information. Additionally, species are differentially sensitive to different types and degrees of disturbance so that this factor interacts with species biology in determining successions. The critical characters of disturbed patches are their size and frequency of occurrence in time. Different kinds of disturbance occur with varying severity in a region and may act jointly to determine the size and configuration of patches.

Two cautions concerning the disturbance regime are in order. First, it is important to know the size and timing of rare, extensive disturbance events as well as normal patches. The effect of rare patches may not be obvious in contemporary time, but it may be critical in the structure and function of natural landscapes (Henry & Swan, 1974). Rare and extreme events can be extremely influential in geomorphic processes (Hack & Goodlett, 1960; Leopold *et al.*, 1964). Second, disturbance regimes will differ among regions as a function of climate, geomorphology and biota. For example, Lorimer (1977) reports that in Maine large-scale disturbances occur at a site in the order of every 800 years for fire and 1150 years for winds. Small-scale disturbances occur every 250–300 years (Lorimer, 1977). In contrast, a given site in Minnesota boreal forests burns every 5–50 years (Heinselman, 1971). These differences must be taken into account when planning for different areas.

Table 1 presents some sizes, causes and frequency of disturbance in North American landscapes. Only references giving measurements or estimates of area of disturbed patches have been selected from the extensive literature on disturbance

TABLE 1
SOME SIZES, CAUSES AND FREQUENCIES OF DISTURBANCE IN NORTH AMERICAN LANDSCAPES

System	Type of disturbance	Mean size	Maximum size	Frequency	Reference
Beech/maple	Windfall	0.010 ha	0.025 ha		Williamson (1975)
Beech/maple	Tornado track		400 m ^b		Lindsay (1972)
Northern deciduous	Wind		15533 ha		Irving in Curtis (1959)
Deciduous	Hurricane	1.61-2.4 km ^b			Beche in Goodlet (1954)
Grassland/forest	Tornado track	77 ha	217 ha	8/yr	Eshelman & Stanford (1977)
Northern deciduous	Hurricane			1635, 1815, 1938 ^c	Spurr (1956)
Deciduous	Flood		60.96 m ^b		Hack & Goodlett (1960)
Deciduous	Landslide	15/24 m ^b	304 m ^b		Hack & Goodlett (1960)
Boreal	Fire		809716 ha		Schmidt (1970)
Pond pine	Fire	11860 ha ^a			Wade & Ward (1973)
Sand hills	Fire	2995 ha ^a			DeCoste <i>et al.</i> (1968)
Boreal	Fire	5922 ha ^a			Sando & Haines (1972)
Montane conifer	Fire	20242 ha ^a			Anderson (1968)
Interior Alaska	Fire (total)	1226 ha		218/yr	Barney (1969)
Interior Alaska	Fire (lightning)	3095 ha		83/yr	Barney (1969)
Boreal	Fire	1739 ha		33/yr	Johnson & Rowe (1975)
Lodgepole/Ponderosa	Fire			0.4/yr	Franklin <i>et al.</i> (1972)
Boreal	Fire			4.8/152700 ha/yr	Martinka (1976)
Montane conifer	Fire	99071 ha ^a			Neiland (1958)

TABLE 1—*contd.*
SOME SIZES, CAUSES AND FREQUENCIES OF DISTURBANCE IN NORTH AMERICAN LANDSCAPES

<i>System</i>	<i>Type of disturbance</i>	<i>Mean size</i>	<i>Maximum size</i>	<i>Frequency</i>	<i>Reference</i>
Pine/spruce/fir	Fire	up to 97% of site showed fire evidence			Patten (1963)
Southern Appalachians	Fire (lightning)	3-4 ha	33 ha	6/400000 ha/yr	Barden & Woods (1973)
Southern Appalachians	Fire (man-made)	5-4 ha			
Mixed conifer	Fire			0.13/yr	Biswell (1967)
Deciduous	Fire	6-6 ha		10/198138 ha/yr	Haines <i>et al.</i> (1975)
Deciduous	Fire	4-4 ha		10/349635 ha/yr	Haines <i>et al.</i> (1975)
Deciduous	Fire	10-4 ha		39/504655 ha/yr	Haines <i>et al.</i> (1975)
Deciduous	Fire	12-6 ha		212/622307 ha/yr	Haines <i>et al.</i> (1975)
Deciduous/fir	Fire	2-0 ha		7/153441 ha/yr	Haines <i>et al.</i> (1975)
Deciduous	Fire	11-1 ha		140/407165 ha/yr	Haines <i>et al.</i> (1975)
Deciduous	Fire	8-1 ha		22/482348 ha/yr	Haines <i>et al.</i> (1975)
Deciduous/conifer	Fire	6-4 ha		148/381255 ha/yr	Haines <i>et al.</i> (1975)
Deciduous/conifer	Fire	3-9 ha		16/495303 ha/yr	Haines <i>et al.</i> (1975)
Deciduous	Fire	12-8 ha		41/198623 ha/yr	Haines <i>et al.</i> (1975)
Deciduous/boreal	Fire	5-0 ha		60/1102024 ha/yr	Haines <i>et al.</i> (1975)
Deciduous/boreal	Fire	1-9 ha		7/319068 ha/yr	Haines <i>et al.</i> (1975)

^a Single event.

^b Width.

^c Years of occurrence.

effects. Disturbances and systems of economic importance, e.g. fires in coniferous forests, are probably over-represented. Some organisms within disturbed patches may survive or rapidly regenerate, but the data give an indication of the kinds and extents of disturbances that may be important for reserve design. Disturbances of various sizes are indicated as important components of system dynamics in many regions (Spurr & Barnes, 1973) even though quantitative estimates of single disturbance events are lacking. Wind in temperate (Goodlett, 1954; Henry & Swan, 1974), and especially tropical, systems (Longman & Jenik, 1974) is important, but disturbance patch sizes are unavailable. Similarly earthquake and landslides are important but areas are unavailable (Dyrness, 1967; DuMontelle *et al.*, 1971; O'Loughlin, 1972).

The biology of the species in a reserve will interact with the disturbance regime to determine extinction probabilities (Simberloff & Abele, 1976*a,b*). Taxa may be differentially sensitive to a given disturbance regime. The mobility of the taxon is an important consideration (Whitcomb *et al.*, 1976). The sedentary nature of many climax (Peterken, 1974) and tropical taxa (Ashton, 1969; Terborgh, 1974*b*) must be taken into account. Whether close competitors require separate patches to avoid extinction should also be determined (Simberloff & Abele, 1976*a*). The requirement of a large resource base by populations of large consumers will affect their minimum area requirements. Resource requirements may be expressed as broad, continuous areas or as areas of concentration ('hot spots', Diamond, 1975*b*), and either may alter in time and space (Willis, 1974). The low population densities of some taxa, particularly in diverse communities, increase local extinction probabilities (Elton, 1975).

The succession within patches after disturbance, i.e. patch longevity, may affect the extinction rates of some taxa. If some species require patches of a given age which support a particular kind of resource (Wright, 1974; Eisenberg & Seidensticker, 1976; Seidensticker, 1976) or do not harbour superior competitors (Pickett, 1976), then sufficient area of such patches must exist in a reserve. Many wildlife species can maintain marginal populations in late successional forests but reach highest population levels only in a mixture of successional habitats. Examples include snowshoe hare ((*Lepus americanus*) Grange, 1965), deer (Byelich *et al.*, 1972) and some Asian ungulates (Eisenberg & Seidensticker, 1976). Gullian & Svoboda (1972) suggest that to maintain highest population levels of ruffed grouse (*Bonasa umbellus*), all age classes of aspen must be available to each wintering and breeding grouse within a normal range of about 4 ha. Knowledge of patch generation and graduation through resource and successional stages is therefore required to preserve such species.

DESIGN CONSIDERATIONS

Island biogeography theory and work on land bridge islands has been used to

generate the following suggestions for nature reserve design. Reserves should be (1) large, (2) circular, (3) undivided, and if divided, (4) connected by dispersal corridors or (5) close to one another (Willis, 1974; Terborgh, 1974*a,b*; Diamond, 1975*a*; Wilson & Willis, 1975; Diamond & May, 1976). Through the additional consideration of patch dynamics which are important in the organisation of natural landscapes, we suggest that the design of nature reserves be based on analysis of 'minimum dynamic area', the smallest area with a natural disturbance regime, which maintains internal recolonisation sources, and hence minimises extinction. The minimum dynamic area of various taxa will undoubtedly differ, however, the minimum dynamic area of a reserve will be defined by the most extinction-prone taxon. Nature reserves should:

- (1) be considerably larger than the largest disturbance patch size, including rare patches,
- (2) include internal recolonisation sources,
- (3) include different ages of disturbance-generated patches,
- (4) encompass areas sufficient to support large consumer populations in habitats not made unsuitable by disturbance, and
- (5) contain separate minimum dynamic areas of each included habitat type.

Direct determination of minimum dynamic area could be made by surveys, similar to those of land bridge islands, for fully relaxed habitat islands, i.e. those which are at equilibrium with respect to their normal disturbance regime. Surveys of habitat islands that may be less than fully relaxed, i.e. those in which the normal disturbance regime has not yet established the new equilibrium (e.g. Galli *et al.*, 1976; Forman *et al.*, 1976) provide minimum area in the absence of disturbance and must be combined with study of patch dynamics to make recommendations on effective reserve size.

ACKNOWLEDGEMENTS

We thank G. Brown for references and comments on the ecology of rare events, F. A. Bazzaz, G. O. Batzli, J. R. Karr, T. D. Lee, M. N. Melampy, J. A. D. Parrish, P. W. Price and A. R. Zangerl for comments, criticism and discussion.

REFERENCES

- ANDERSON, H. E. (1968). *Sundance fire: An analysis of fire phenomena*. Ogden, Utah, USDA For. Serv. Intermountain Forest and Range Expt. Station.
- ASHTON, P. S. (1969). Speciation among tropical forest trees. Some deductions in the light of recent evidence. *Biol. J. Linn. Soc.*, 1, 155-96.
- BARDEN, L. S. & WOODS, F. W. (1973). Characteristics of lightning fires in southern Appalachian forests. *Proc. Ann. Tall Timber Fire Ecol. Conf.*, 13, 345-61.

- BARNEY, R. J. (1969). *Interior Alaska wildfires 1956-1965*. Pacific Northwest Forest & Range Experiment Station, USDA For. Serv. Institute of Northern Forestry, Juneau, Alaska.
- BISWELL, H. H. (1967). Forest fire in perspective. *Proc. Ann. Tall Timbers Fire Ecol. Conf.*, **7**, 43-64.
- BRATTON, S. P. (1975). The effect of the European wild boar (*Sus scrofa*) on gray beech forest in Great Smoky Mountains National Park. *Ecology*, **56**, 1356-66.
- BRAY, J. R. (1956). Gap phase replacement in maple-basswood forest. *Ecology*, **37**, 598-600.
- BYELICH, J. D., COOK, J. L. & BLOOCH, R. I. (1972). Management for deer. *Aspen: Symp. Proc. USDA For. Serv. Gen. Tech. Report NC-1*, 120-5. North Central Forest Experimental Station.
- CURTIS, J. T. (1959). *The vegetation of Wisconsin*. Madison, Wisconsin, University of Wisconsin Press.
- DECOSTE, J. H., WADE, D. D. & DEEMING, J. E. (1968). The Gaston fire. *Southeast. For. Expt. Sta. USDA For. Serv. Res. Pap. SE-43*, 36 pp.
- DIAMOND, J. M. (1972). Biogeographic kinetics: Estimation of relaxation times for avifaunas of southwest Pacific Islands. *Proc. natn. Acad. Sci. USA*, **69**, 3199-203.
- DIAMOND, J. M. (1975a). The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biol. Conserv.*, **7**, 129-46.
- DIAMOND, J. M. (1975b). Assembly of species communities. In *Ecology and evolution of communities*, ed. by M. L. Cody & J. M. Diamond, 342-444. Cambridge, Belknap Press of Harvard University.
- DIAMOND, J. M. (1976). Island biogeography and conservation: Strategy and limitations. *Science, N.Y.*, **193**, 1027-9.
- DIAMOND, J. M. & MAY, R. M. (1976). Island biogeography and the design of natural reserves. In *Theoretical ecology*, ed. by R. M. May, 163-86. Philadelphia, Saunders.
- DUMONTELE, P. B., HESTER, N. C. & COLE, R. E. (1971). Landslides along the Illinois River valley south and west of La Salle and Peru, Illinois. *Environmental Geology Notes*, No. 48. Illinois State Geological Survey, Urbana, Ill.
- DYRNESS, C. T. (1967). Mass soil movement in the H. J. Andrews Experimental Forest. *U.S. For. Serv. Res. Pap. PNW-4L*, 12 pp.
- EISENBERG, J. F. & SEIDENSTICKER, J. (1976). Ungulates in southern Asia: A consideration of biomass estimates for selected habitats. *Biol. Conserv.*, **10**, 293-308.
- ELTON, C. S. (1975). Conservation and the low population density of invertebrates inside neotropical rain forest. *Biol. Conserv.*, **7**, 3-15.
- ESHELMAN, S. & STANFORD, J. L. (1977). Tornadoes, funnel clouds and thunderstorm damage in Iowa during 1974. *Iowa State J. Res.*, **51**, 327-61.
- FORCIER, L. K. (1975). Reproductive strategies and the co-occurrence of climax tree species. *Science, N.Y.*, **189**, 808-10.
- FORMAN, R. T. T., GALLI, A. E. & LECK, C. F. (1976). Forest size and avian diversity in New Jersey woodlots with some land use implications. *Oecologia*, **26**, 1-8.
- FRANKLIN, J. F., HALL, F. C., DYRNESS, C. T. & MASER, C. (1972). *Federal research natural areas in Oregon and Washington. A guidebook for scientists and educators*. Portland, Oregon, Pacific N.W. Forest and Range Experimental Station.
- GALLI, ANNE E., LECK, C. F. & FORMAN, R. T. T. (1976). Avian distribution patterns in forest islands of different sizes in central New Jersey. *Auk*, **93**, 356-64.
- GEIST, V. (1971). *Mountain sheep: A study in behavior and evolution*. Chicago, University of Chicago Press.
- GOODLETT, J. C. (1954). Vegetation adjacent to the border of the Wisconsin drift in Potter County, Pennsylvania. *Harv. For. Bull.*, **25**.
- GRANGE, W. (1965). Fire and tree growth relationships to snowshoe rabbits. *Proc. Ann. Tall Timber Fire Ecol. Conf.*, **4**, 111-25.
- GULLION, G. W. & SVOBODA, F. J. (1972). The basic habitat resource for ruffed grouse. *Aspen: Symp. Proc. USDA, For. Serv. Gen. Tech. Report NC-1*. 113-19. North Central Forestry Experiment Station.
- HACK, J. T. & GOODLETT, J. C. (1960). Geomorphology and forest ecology of a mountain region in the central Appalachians. *Prof. Pap., U.S. Geol. Surv.* No. 347.
- HAINES, D. A., JOHNSON, V. J. & MAIN, W. A. (1975). Wildfire atlas of the north central states. *USDA For. Serv. Gen. Tech. Pap. NC-16*.
- HARPER, J. L. (1965). Establishment, aggression and cohabitation in weedy species. In *The genetics of colonizing species*, ed. by H. G. Baker and G. L. Stebbins, 243-65. New York, Academic Press.
- HEINSELMAN, M. L. (1971). The natural role of fire in northern conifer forests. In *Fire in the northern environment*, 61-72. Portland, Oregon, Pacific Northwest Forest and Range Experiment Station USDA Forest Service.

- HENRY, J. D. & SWAN, J. M. A. (1974). Reconstructing forest history from live and dead plant material—An approach to the study of forest succession in southwest New Hampshire. *Ecology*, **55**, 772–83.
- HORN, H. S. (1976). Succession. In *Theoretical ecology principles and applications*, ed. by R. M. May, 187–204. Philadelphia, Saunders.
- HOUSTON, D. B. (1971). Ecosystems of national parks. *Science, N.Y.*, **172**, 648–51.
- JOHNSON, E. A. & ROWE, J. S. (1975). Fire in the subarctic wintering ground of the Beverley caribou herd. *Am. Midl. Nat.*, **94**, 1–14.
- JONES, E. W. (1945). The structure and reproduction of the virgin forests of the north temperate zone. *New Phytol.*, **44**, 130–48.
- LEOPOLD, L. B., WOLMAN, M. G. & MILLER, J. P. (1964). *Fluvial processes in geomorphology*. San Francisco, Freeman.
- LEVIN, S. A. (1976). Population dynamic models in heterogeneous environments. *Ann. Rev. Ecol. Syst.*, **7**, 287–310.
- LINDSAY, A. A. (1972). Tornado tracks in the presettlement forests of Indiana. *Proc. Indiana Acad. Sci.*, **82**, 181 (Abstr.).
- LONGMAN, K. A. & JENÍK, J. (1974). *Tropical forest and its environment*. London, Longman.
- LORIMER, C. G. (1977). The presettlement forest and natural disturbance cycle of northeastern Maine. *Ecology*, **58**, 139–48.
- LOUCKS, O. L. (1970). Evolution of diversity, efficiency and community stability. *Am. Zool.*, **10**, 17–25.
- MACARTHUR, R. H. & WILSON, E. O. (1967). *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey.
- MARTINKA, C. J. (1976). Fire and elk in Glacier National Park. *Proc. Tall Timber Fire Ecol. Conf.*, **14**, 377–89.
- MATTSON, W. J. & ADDY, N. D. (1975). Phytophagous insect as regulators of forest primary production. *Science, N.Y.*, **190**, 515–22.
- MCLEAN, A. (1976). Protection of vegetation in ecological reserves in Canada. *Can. Fld Nat.*, **90**, 144–8.
- MEIJER, W. (1973). Devastation and regeneration of lowland dipterocarp forests in south-east Asia. *BioScience*, **23**, 528–33.
- NEILAND, B. J. (1958). Forest and adjacent burn in the Tillamook burn area of northwestern Oregon. *Ecology*, **39**, 660–71.
- OLD, S. M. (1969). Microclimates, fire, and plant production in an Illinois prairie. *Ecol. Monogr.*, **39**, 355–84.
- O'LOUGHLIN, C. L. (1972). A preliminary study of landslides in the coast mountains of southwestern British Columbia. In *Mountain geomorphology: Geomorphological processes in the Canadian Cordillera*, ed. by H. O. Ataymayker and H. J. McPherson, 101–11. *B. C. Geographical Series*, No. 14. Vancouver, Tantalus Research Ltd.
- PATTEN, D. T. (1963). Vegetational pattern in relation to environments in the Madison Range, Montana. *Ecol. Monogr.*, **33**, 375–406.
- PETERKEN, G. F. (1974). A method of assessing woodland flora for conservation using indicator species. *Biol. Conserv.*, **6**, 239–45.
- PICKETT, S. T. A. (1976). Succession: An evolutionary interpretation. *Am. Nat.*, **110**, 107–19.
- PLATT, W. J. (1975). The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. *Ecol. Monogr.*, **45**, 285–305.
- ROOT, R. B. (1975). Some consequences of ecosystem texture. In *Ecosystem analysis and prediction*, ed. by S. A. Levin, 83–92. Philadelphia, Society for Industrial and Applied Mathematics.
- SANDO, R. W. & HAINES, D. A. (1972). Fire weather and behavior of the Little Sioux fire. *USDA For. Serv. Res. Pap. NC-76*, 6 p. North Central Forest Experiment Station, St Paul, Minn.
- SCHMIDT, R. L. (1970). A history of pre-settlement fires on Vancouver Island as determined from Douglas fir ages. In *Tree ring analysis with special reference to northwest America*. *Univ. B. C. Fac. For. Bull.*, **7**, 107–8.
- SEIDENSTICKER, J. (1976). Ungulate populations in Chitawan Valley, Nepal. *Biol. Conserv.*, **10**, 183–210.
- SICCAMA, T. G., WEIR, G. & WALLACE, K. (1976). Ice damage in a mixed hardwood forest in Connecticut in relation to *Vitis* infestation. *Bull. Torrey bot. Club*, **103**, 180–3.
- SIMBERLOFF, D. S. (1974). Permo-Triassic extinctions: The effects of area on biotic equilibrium. *J. Geol.*, **82**, 267–74.
- SIMBERLOFF, D. S. & ABELE, L. G. (1976a). Island biogeography theory and conservation practice. *Science, N.Y.*, **191**, 285–6.
- SIMBERLOFF, D. S. & ABELE, L. G. (1976b). Island biogeography and conservation: strategy and limitations. *Science, N.Y.*, **193**, 1032.

- SPRUGEL, D. G. (1976). Dynamic structure of wave-generated *Abies balsamea* forests in the northeastern United States. *J. Ecol.*, **64**, 889–911.
- SPURR, S. H. (1956). Natural restocking of forests following the 1938 hurricane in central New England. *Ecology*, **37**, 443–51.
- SPURR, S. H. & BARNES, B. V. (1973). *Forest ecology*, 2nd edition. New York, Ronald Press.
- STONE, E. C. (1965). Preserving vegetation in parks and wilderness. *Science, N.Y.*, **150**, 1261–7.
- TERBORGH, J. (1974a). Preservation of natural diversity: The problem of extinction prone species. *BioScience*, **12**, 715–22.
- TERBORGH, J. (1974b). Faunal equilibria and the design of wildlife preserves. In *Tropical ecological systems. Trends in terrestrial and aquatic research*, ed. by F. B. Golley and E. Medina, 369–80. New York, Springer Verlag.
- TERBORGH, J. (1976). Island biogeography and conservation: Strategy and limitations. *Science, N.Y.*, **193**, 1029–30.
- THOMPSON, J. N. (in press). Patch dynamics in *Pastinaca sativa* and resource availability to a specialized herbivore.
- VOGL, R. J. & SCHORR, P. K. (1972). Fire and manzanita chaparral in the San Jacinto Mountains, California. *Ecology*, **53**, 1179–88.
- WADE, D. D. & WARD, D. E. (1973). An analysis of the Air Force bomb range fire. *Southeast. For. Exp. Sta., USDA For. Serv. Res. Pap. SE-105*. 38 pp.
- WALTER, H. (1971). *Vegetation of the earth*. New York, Springer-Verlag.
- WEBB, L. J. (1958). Cyclones as an ecological factor in tropical lowland rain forest, North Queensland. *Austr. J. Bot.*, **6**, 220–8.
- WHITCOMB, R. F., LYNCH, J. F., OPLER, P. A. & ROBBINS, C. S. (1976). Island biogeography and conservation: Strategy and limitations. *Science, N.Y.*, **193**, 1030–2.
- WHITTAKER, R. H. (1953). A consideration of climax theory: The climax as a population and pattern. *Ecol. Monogr.*, **23**, 41–78.
- WILLIAMSON, G. B. (1975). Pattern and seral composition in an old-growth beech-maple forest. *Ecology*, **56**, 727–37.
- WILLIS, E. O. (1974). Populations and local extinctions of birds on Barro Colorado Island, Panama. *Ecol. Monogr.*, **44**, 153–69.
- WILSON, E. O. (1969). The species equilibrium. *Brookhaven Symp. Biol.*, **22**, 38–47.
- WILSON, E. O. & WILLIS, E. O. (1975). Applied biogeography. In *Ecology and evolution of communities*, ed. by M. L. Cody and J. M. Diamond, 522–34. Cambridge, Belknap Press of Harvard University.
- WRIGHT, H. E. (1974). Landscape development, forest fires, and wilderness management. *Science, N.Y.*, **186**, 487–95.
- WRIGHT, H. M. (1974). Non-game wildlife and forest management. In *Wildlife and forest management in the Pacific northwest*, ed. by H. C. Black, 27–38. Corvallis, Forest Research Laboratory School of Forestry, Oregon State University.