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DANCING WITH FIRE: ECOSYSTEM DYNAMICS, MANAGEMENT, AND THE KARNER BLUE (LYCAEIDES MELISSA SAMUELIS NABOKOV) (LYCAENIDAE)

Additional key words: conservation, endangered species, metapopulation dynamics, sand and oak barrens, savanna, prescribed burning.

The recent listing of the Karner Blue Butterfly (*Lycaeides melissa samuelis* Nabokov) as an endangered species (Clough 1992) has increased interest in managing and restoring populations of this charismatic invertebrate. The Karner Blue and other lepidopteran species are rapidly becoming symbols for restoring and conserving the barrens/savanna ecosystems that occur on well drained sand deposits in the Great Lakes Region and New England. The dynamic processes that produced unique botanical communities also produced a highly specialized community of invertebrates adapted to this regime. Because of their general biological requirements, invertebrates are often closely linked to a few key ecological resources, such as specific soil types, edaphic conditions and/or individual host-plant species or genera (Panzer et al. 1995).

The importance of oak barrens/savanna habitats to invertebrates is well illustrated by the Lepidoptera. In Ohio, the only midwestern state with a completed state-wide survey of all Lepidoptera species, the Oak Openings, Ohio's only oak barrens/savanna community, supports the largest assemblage of imperiled butterflies and moths in the state. For example, five species of imperiled butterflies and 17 species of owlet moths (Noctuidae) occur in the Oak Openings, representing approximately 4% and 3% respectively, of the resident species in Ohio (Shuey et al 1987a, 1987b, Metzler & Lucas 1990, Iftner et al. 1992, Rings et al. 1992). The maintenance of this ecosystem is vital for the preservation of lepidopteran



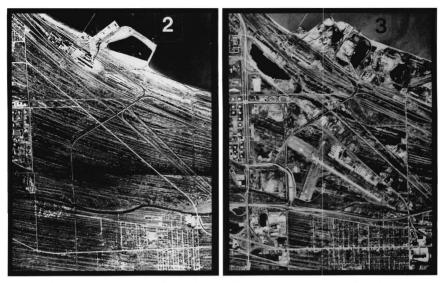
FIG. 1. Karner blue habitat: oak barrens in Newago County, Michigan. Note the sunlit, grass-dominated opening surrounded by oak woodlands and numerous, fire-stunted oak and jackpine saplings within the clearing.

biodiversity, as well as for other lesser known plants and animals in Ohio and the importance of oak barrens/savanna communities to biodiversity maintenance in the other Great Lakes States is certainly similar to the situation in Ohio. For example, Panzer et al. (1995) list 17 species of butterflies that are primarily restricted to sand prairie, savanna and xeric prairie in the greater Chicago region.

The decline of oak barrens/savanna lepidopteran communities can be attributed to several factors, but habitat loss, the disruption of ecosystem level processes and patch dynamics, and the collapse of metapopulation dynamics of many species are generally the primary contributors. Here I discuss these intertangled processes, and the management implications and problems associated with each process as they relate to the Karner Blue (for ecological information regarding other imperiled midwestern lepidopteran species, see the species and habitat accounts in Rings et al. 1992 and Iftner et al. 1992).

Habitat loss and fragmentation resulting from physical alteration. Habitat loss is often the most easily implicated factor contributing to the decline of most imperiled invertebrate species (Hafernik 1992) and the Karner Blue is no exception. To persist locally, Karner Blue populations require relatively large stands of the hostplant, blue lupine (Lupinus perennis L.) (Opler & Krizek 1984). Habitats supporting the butterfly are generally open and sunny with scattered trees and shrubs (Fig. 1), and are dominated by grasses and other herbaceous species growing in well drained, sandy soils—in other words, healthy barrens/savanna communities (Zaremba & Pickering 1994). Oak barrens/savanna loss can be attributed to several factors, ranging from outright destruction to more subtle secondary impacts such as the encouragement of forest growth in areas of urban encroachment.

Oak barrens/savannas have been subject to the same trends that altered almost every ecosystem in eastern North America. The expansion of agriculture into new ecosystems was largely a process of trail and error: farming sand barrens was an error. In the trial process, many habitats were altered or destroyed and the local hydrology was often modified.



FIGS. 2–3. Fragmentation of the dune and swale ecosystem (including dune-top oak barrens) of southern Lake Michigan. 2, the system in 1938. 3, the system as it appeared in 1994. Note the fragmentation and almost complete isolation of the remaining dune and swale fragments, surrounded by urban/industrial Gary and Hammond, Indiana. Scattered throughout this complex are habitats that support or have the potential to support the Karner blue. Fig. 2 courtesy of the Indiana Geological Survey.

This trial process came to a halt during the prolonged drought of the 1930's, when it became apparent that the infertile soils of these communities could not support sustainable agricultural production.

The unfortunate location of many regional barrens/savanna communities also contributed to their destruction, especially in New England. For example the Albany Pine Barrens sit adjacent to the city of Albany, New York, and the expansion of the city has, and still is contributing to the urbanization of this ecosystem (Dirig 1994). The Oak Openings ecosystem in Ohio is suffering the same fate as Toledo suburbs expand (Iftner et al. 1992, Grigore & Windis 1994); And the complex dune and swale communities which once lined southern Lake Michigan have been almost eliminated by industrialization and urbanization (Figs. 2 and 3).

On a broader scale, the infertility of the sand soils themselves has led to the destruction of sand barrens communities. Many abandoned farms located in oak barrens/savanna ecosystems eventually reverted to federal and state ownership (via tax defaults), largely to become public forest land. Because the preservation of non-forest communities was not a high priority of national or state forests in the 1930's through the present, many oak barrens/savanna communities were converted into 'productive' use by conversion to pine plantations. These monocultures of stressed trees bear witness to the incomplete and short-sighted ecological planning of past eras. Degraded barrens communities continue to be primary targets for new developments such as industrial parks and residential communities, possibly because the cost associated with acquiring barrens land is less than the cost for purchasing 'productive' agricultural lands.

Habitat loss and fragmentation resulting from the disruption of ecosystem level processes and patch dynamics. Closely related to the impact of habitat loss is the elimination of ecosystem level processes. Oak barrens/savanna communities are among the most dynamic in the Midwest—the open habitats that support the Karner Blue

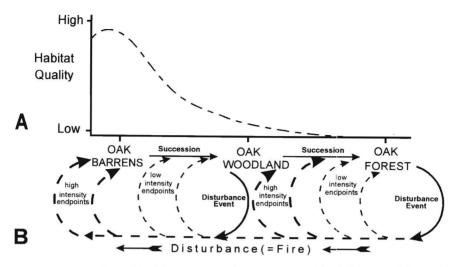


FIG. 4. A simple model of the interaction between Karner blue habitat suitability, oak barrens succession, and fire disturbance. A: Optimal Karner blue habitat is early successional oak barrens; as succession proceeds, habitats become shaded and habitat quality decreases. B: Oak barrens, in the absence of disturbance, convert through succession to oak woodland/oak forest communities. Note that while fire and other disturbances can re-set succession to an earlier state, the exact outcome depends upon fire (disturbance) intensity and other mitigating factors. In the absence of disturbance, Karner blue habitat is eventually lost.

were originally maintained by a steady procession of wildfires, which killed woody invasive plants while favoring fire-adapted dune and savanna communities. Without fire disturbance, shade tolerant and fire sensitive species increase in density, and open barrens and savanna species decline.

Functional oak barrens/savanna communities are in a constant but dynamic flux. Succession pushes the community towards an association characterized by fire intolerant woody and shade tolerant herbaceous species, while fire disturbance realigns the community towards fire tolerant and shade intolerant species (Fig. 4). The original patch dynamics of these communities was in constant flux, and individual sites supported communities that reflected recent disturbance history. Although fire may have been a yearly occurrence within oak barrens/savanna ecosystems, the spatial distribution of the fire was less predictable. For example, in the Albany Pine Barrens the point fire frequency may have ranged between 6 to 18 years, with a likely average frequency of once every 10 years (Givnish et al. 1988). Thus, these communities were composed of a constantly changing patchwork of habitats, reflecting the hit or miss nature of recent wildfires. Interdispersed through this patchwork were the recently disturbed sites supporting Karner Blue populations.

Unfortunately, our society tends to abhor wildfire because of the perceived destructive nature of fire. Thus, oak barrens/savanna ecosystems adjacent to urbanized areas are subject to routine/reflexive fire suppression and state and national forests routinely suppress wildfires on their lands. With few positive attributes to associate with wildfire, active ecosystem management still remains controversial to the general public in many areas. Thus, society generally deprives these ecosystems of the very force that created them, a predictable and frequent fire disturbance regime.

Urban and agricultural encroachment, in addition habitat elimination, fragment barrens/savanna communities by inserting non- or less-flammable land uses into a highly flammable ecosystem (Givnish et al. 1988). These barriers limit the occasional wildfire to small land tracts, reducing the potential for naturally spreading wildfire to maintain the ecosystem in an early successional state. In addition, urban encroachment increases the difficulty of using controlled burns to manage oak barrens/savanna communities because of the liability and perceived danger/nuisance to residents.

Without the influence of a disturbance regime, oak barrens/savanna communities have succumbed to other community types. The impact of fire suppression on these communities has been as great or greater than outright habitat destruction in most areas. For example, oak barrens are critically endangered and the Karner Blue is extirpated from Ohio's Oak Openings, despite the "preservation" of over 9000 acres by state, local and private organizations. Most of the habitats in the Oak Openings which once may have supported oak barrens/savanna have converted to young oak forest. Similarly, what remains of the Albany Pine Barrens in New York has converted into a largely overgrown ecosystem (Givnish et al. 1988). At its worst, land is dominated by black locust forests; at its best, dense scrub oak brushland is dominant.

Disruption of metapopulation dynamics. The plants and animals that together form oak barrens/savanna communities are adapted to the ecosystem level processes which originally structured these communities. To persist regionally in this dynamic ecosystem type, invertebrates must cope with both the ecosystem patch dynamics as well as the forces driving patch dynamics. In simple terms, invertebrates populations must shift locations as quality habitats become available/unavailable and they must be able to survive wildfire, either directly or indirectly. While healthy metapopulations of the Karner Blue may seem to occupy entire barrens/savanna ecosystems, individual sub-populations are usually highly localized and isolated from neighboring populations by barriers of unsuitable habitat. These isolated sub-populations are vulnerable to extinction from both community succession and ecosystem disturbance regimes.

Unfortunately, the Karner Blue is not well adapted to survive fire directly (e.g., Iftner et al. 1992, Swengel 1994). The very mechanism critical for creating and maintaining habitat for this species, fire, also kills all life stages of the butterfly (although there is emerging evidence that the Karner Blue may occasionally survive cool, low fuel-load fires, but requires better documentation). Recently burned habitats must be colonized or recolonized by individuals immigrating from nearby or adjacent habitats. Confounding this is the limited dispersal abilities of the adults. Givnish et al. (1988) estimate that maximum dispersal distance for colonization of unoccupied habitats is approximately 0.5 miles. This agrees closely with values obtain in North Wales for the ecologically similar and related butterfly, Plebejus argus in North Wales (Thomas & Harrison 1992): i.e., metapopulation dynamics of P. argus over a seven year period indicated that the likelihood of colonizing suitable habitats decreased rapidly in habitats more than 1 km away from potential source populations. These authors concluded that if the continuity of suitable habitat distribution was broken within an ecosystem, entire metapopulations of P. argus were likely to collapse.

Because most oak barrens/savanna communities are suffering from the effects of fire suppression, optimal Karner Blue habitats are generally limited in size and widely dispersed. This combination of reduced optimal habitat patch size combined with increased distance between optimal habitat patches has disrupted the metapopulation dynamics of the Karner Blue. For example, suitable but unoccupied habitats may not have a nearby Karner Blue source population from which colonization is possible. Likewise, occupied habitats may require recolonization following fires; recolonization has become less likely as the distance separating occupied habitats increases. In effect, the rate of localized population extinction has been accelerated by declining habitat suitability and size, while the odds of new colonization events have declined as optimal habitats become increasingly fragmented due to succession and alteration. This disruption of metapopulation dynamics is currently causing the downward spiral of several metapopulations of the Karner Blue, even as regional attempts to restore these ecosystems proceed.

The dance with fire. For the Karner Blue, the interplay between habitat suitability, habitat distribution and patch dynamics, metapopulation dynamics and metapopulation persistence is complex. This is best illustrated by the historical distribution of the butterfly itself. The ecosystems known to support metapopulations of this butterfly are generally

large, measured in tens of thousands of acres. Smaller sand barren/oak savanna complexes are less likely to have supported Karner Blues in historic times. This is probably a reflection chance interplays between ecosystem processes and metapopulation dynamics: the larger the ecosystem, the better the odds that all the pieces fall together and populations persist. Smaller ecosystems may have provided fewer opportunities for population persistence, and Karner Blue populations did not persist to historic times. As Givnish et al. (1988) poetically state, persistent populations exist as a "flickering mosaic of Karner Blue populations, with some going extinct in a given area as others are being founded on sites recently burnt by colonists from sites burnt a somewhat longer time ago." In smaller ecosystems, these populations may simply flicker out.

However, given that almost every oak barrens/savanna community in the Midwest must now be actively managed to persist, much of the element of chance can be removed from Karner Blue management. With intensive management, which includes carefully planned burn units to create suitable habitats, Karner Blue populations should be manageable on preserves as small as 200 acres. At this scale, management would have to be almost mechanical, with approximately 10–15% of the entire land-base burned annually, and the burn units configured to provide adequate dispersal opportunities for Karner Blues. Larger areas could be managed less mechanically, but would still require carefully planned management activities. Small management units could be used to establish core populations within larger ecosystem management areas, from which dispersing butterflies could become more widely established.

Finally, to protect against catastrophic disaster, several independent sets of Karner Blue populations should be maintained in each oak barrens/savanna ecosystem. Because of the flammable nature of the ecosystems, true wildfires that consume thousands of acres at one time are a reality. Because individual Karner Blue populations may succumb to such an event, independent core populations should be dispersed through the ecosystem to ensure that single catastrophic events cannot eliminate entire metapopulations.

Preserve managers and stewards must struggle to re-establish the processes that created the barrens and savanna ecosystems they manage. If the Karner Blue is to survive, we must literally take it back to the big dance, where metapopulations swirled with patch dynamics to the music of fire. By managing remnant barrens and savanna communities in light of large-scale ecosystems processes, it should be possible to preserve not only the Karner Blue, but the untold other inconspicuous life-forms adapted to these ever changing ecosystems.

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LIFE HISTORY NOTES FOR THE PALLID EMPEROR MOTH, CIRINA FORDA (SATURNIIDAE) IN NIGERIA

Additional key words: phenology, hostplants, Africa.

Cirina forda Westwood has long been known as a serious pest of the sheanut tree, Vittelaria paradoxa (Sapotaceae) in Nigeria (Golding 1929). Packard (1914) described the larva, and Boorman (1970) and Leleup and Beams (1969) provided brief accounts of the biology and phenology of this moth. Leleup and Deams (1969) reported Erythropheum africanum as a larval host in northern Zaire, but that the tree does not occur in Nigeria. The dried larvae of C. forda are referred to locally as "manimani," and are of economic