

REFUGIA FROM BROWSING AS REFERENCE SITES FOR RESTORATION PLANNING

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In the western U.S., deciduous woody species along riparian systems provide important ecological functions. For example, they stabilize stream banks and impart hydraulic resistance during overbank flows, enhance deposition of organic matter and fine sediment on floodplains, support general food webs of aquatic and riparian organisms, moderate water temperatures and microclimates, and recruit large wood (National Research Council 2002b). Measures of biodiversity, biomass, and number of rare species are often much greater in riparian habitats than on adjacent uplands (Knopf et al. 1988). Deciduous woody species on upland sites provide for watershed protection, aesthetics, wood fiber, and habitats that also help support a wide variety of wildlife and avian species (Bartos 2001, National Research Council 2002a).

Despite their significance to western ecosystems, deciduous woody species have been in decline (Braatne et al. 1996, Kay 1997, Bartos 2001). Many western riparian systems have been diminished in total area (Swift 1984) while many that remain often have been altered or degraded by various human activities and land uses (Wigington and Beschta 2000).

While the causes of loss and alteration of woody species during a period of increasing Euro-American influence are multiple, high levels of herbivory from domestic ungulates have often degraded ecosystem structure and function. Such degradation includes impacts to habitats of numerous species of vertebrates and invertebrates, various food web interactions, and nutrient cycling (Fleischner 1994, Braatne et al. 1996, Belsky and Blumenthal 1997, Donahue 1999, Rooney and Waller 2003). Even where land has been set aside within the National Park system, native ungulates some-

times have had significant impacts on vegetation (National Research Council 2002a). Thus, there is an increased need for restoration of deciduous woody species at landscape scales. Such restorations would be facilitated if reference sites existed that were relatively unimpacted by ungulate herbivory (i.e., refugia) since they (1) can provide an understanding of vegetation dynamics without the effects of herbivory, (2) help define the degree and extent of degradation in woody plant communities for other portions of a landscape, (3) may assist in setting restoration priorities, and (4) may provide important “targets” for restoration programs.

In landscapes that have experienced the effects of widespread and sustained herbivory from ungulates (either domestic or wild), refugia from browsing can be created with fenced exclosures (Brookshire et al. 2002, Sarr 2002), provided that sufficient seed or bud banks remain. Unfortunately, such exclosures are seldom available. Yet, even within a heavily browsed landscape we suggest there will often exist scattered refugia sites with deciduous woody species; such sites are often small in area but may contain a relatively diverse plant community structure and composition. Where such refugia have persisted is notable as they typically occur in locations where there are multiple impediments to ungulate access. The importance of these sites is that they provide a glimpse of the potential structure and composition of plant communities where ungulate herbivory is not of overriding significance and may represent an initial approximation of what other areas in a landscape might become if herbivory levels were reduced or curtailed. Because refugia are often visually different (e.g., high contrast, taller plants, higher plant

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densities) relative to the general landscape, they are typically easy to locate. In the following discussion, we identify numerous types of “impediments” to browsing that have contributed to the maintenance of refugia.

Several studies have described the role of natural physical barriers to animal movement in creating refugia. At the microsite scale, Rooney (1997) described how herbaceous vegetation growing on the tops of boulders escaped deer browsing. Schreiner et al. (1996) discovered shrub refugia behind log barriers created by fallen conifers in Olympic National Park. They found several species of shrubs in these refugia that successfully produced flowers and fruit unlike the majority of the shrubs growing nearby in the open. They concluded that these refugial shrub patches may provide critical seed sources for recolonization of the floodplain by species that might otherwise be absent. Ripple and Larsen (2001) found that fallen conifers killed by the 1988 fires in Yellowstone National Park could be dense enough to provide local refugia, allowing aspen recruitment with high levels of ungulate browsing nearby (Fig. 1). Beschta and Ripple (2005) identified increased cottonwood recruitment occurring between highways and terrain features such as steep slopes and rivers that reduced the presence of animals. Larsen and Ripple (2003) discovered a lack of aspen recruitment across the northern range in Yellowstone National Park except for stands growing in the midst of scree deposits. They concluded that the scree protected the aspen from ungulate browsing. The scale of the refugia in the above case studies ranges from 1 to several thousand square meters. Yet, physical barriers also have been described at much larger scales where terrain features such as mesas and buttes impeded ungulate access and created refugia (Jameson et al. 1962, Ambos et al. 2000).

It is important to recognize that the widespread loss of major predators such as wolves (*Canis lupus*) early in the 20th century allowed ungulates to browse with a reduced threat of predation. In addition to the often widespread effects of domestic ungulates, woody plant communities can be profoundly affected by native ungulates when top predators are removed from ecosystems (Leopold et al. 1947, Terborgh et al. 1999, Ripple and Larsen 2000, Beschta 2003, Soulé et al. 2003) and evidence is growing on the importance of predator con-

servation because of cascading effects upon lower trophic levels (Smith et al. 2003, Ripple and Beschta 2004). Refugia created through risk-sensitive foraging involve predator/prey interactions whereby areas of low browsing intensity occur, either in conjunction with existing physical barriers or independent of them. Changes in prey behavior due to the presence of predators are referred to as predation-risk effects. These behavioral modifications include changes in habitat use, patch selection, and choices of feeding sites (Lima and Dill 1990). This process can produce low populations of herbivores in a predator’s core use area, thus creating refugia for woody browse species through lower herbivory. For example, in response to the presence of predators, researchers have documented increased concentrations of ungulates in buffer zones away from both mammalian predators (Mech 1977, White et al. 1998, Ripple et al. 2001) and human hunters (Laliberte and Ripple 2003).

Predation-risk effects on prey animals, in combination with varying terrain conditions, can also create “invisible impediments” to browsing and have apparently been caused by sport hunters as well as wolves. For example, St. John (1995) concluded that aspen stands within 500 m of roads were less impacted by wild ungulates than those farther away, suggesting that elk adjusted their foraging behavior to avoid human contact and possible predation by humans. Other researchers found that aspen were heavily browsed on U.S. Air Force land that was utilized year-round by a large elk population but where sport hunting was not permitted. Conversely, this property is surrounded by national forest land where hunting is allowed and the aspen stands were minimally browsed (McCain et al. 2003).

Ripple and Beschta (2003) proposed that, following the reintroduction of wolves in Yellowstone National Park, a “terrain fear factor” has been playing an important role in the selective release of cottonwood and willow from long-term browsing suppression by elk. In their predation-risk hypothesis, they suggested that elk would increasingly forage at sites that allow early detection, avoidance, and successful escape from wolves. They found cottonwood and willow to be releasing at potentially high-risk sites with limited visibility of approaching wolves and/or with terrain impediments to escape from an attack, such as



Fig. 1. Protected aspen sprouts growing among coarse woody debris on the Blacktail Plateau in Yellowstone National Park (example of a physical barrier to browsing). See Ripple and Larsen (2001) for details on aspen recruitment in locations where dead trees have created a jackstraw barrier to ungulate movement. In 2003 the aspen sapling to the left of the white pole was approximately 4 m tall (see arrow), while aspen sprouts growing nearby outside the woody debris were less than 1 m tall.

high terraces, steep cutbanks, and nearby gullies (Fig. 2).

There are several limitations to the use of refugia as reference sites. Because they are typically of limited size and spatial distribution, their locations may not be representative of the broader landscape (i.e., different abiotic conditions, geographically or topographically biased). In such situations they provide little opportunity for developing statistical inferences. Refugia may maintain certain rare species, but in some cases overall community composition and functioning can be different from the larger landscape in need of restoration. Information identifying the historical level of ungulate use often is lacking for these sites, and levels of browsing may be occurring, of which a certain amount would represent a natural condition (e.g., Schreiner et al. 1996). Finally, a total lack of browsing (such as a fenced enclosure) might

represent atypical conditions for pre-European plant communities.

Realizing the potential limitations of local refugia as examples of these conditions, we nevertheless suggest that the identification and use of refugia can be important in understanding the role of ungulate herbivory on western landscapes and their potential for recovery. We propose 3 situations where refugia for deciduous woody browse species are likely to persist: (1) Where the browsing is predominantly from domestic ungulates, physical barriers to site access will control the occurrence of refugia. (2) Where wild ungulates are present but natural predators are not, both physical barriers and predation risk associated with human hunting will tend to control the occurrence of refugia. (3) Where natural predators have a significant presence, physical barriers and terrain features that affect the perceived



Fig. 2. Willow and cottonwood recruitment occurring on an island of the Lamar River in northern Yellowstone National Park. This island is considered to be an area of high predation risk (example of an invisible impediment to browsing). See Ripple and Beschta (2003) for details on how the plants on this island were released, due to changes in elk browsing patterns, after the reintroduction of wolves in the mid-1990s. In contrast, stream banks in the low-predation-risk area extending from the island toward the distant mature cottonwood stands on the floodplain (right center of photograph) have no recruiting willows or cottonwood. The mature cottonwood stands also occupy low-risk sites, and cottonwood recruitment was essentially terminated after wolves were extirpated from the park in the mid-1920s (Beschta 2003).

predation risk of prey animals at varying spatial scales will influence the number, size, and spatial distribution of refugia. While the occurrence of refugia may be sufficiently common in some landscapes to provide adequate reference sites for restoration purposes, additional sites could be targeted for livestock or native ungulate exclusion using fenced exclosures to ensure a full portfolio of reference sites. In some extreme cases, refugia might be the only places where certain native species still occur, and these sites can serve as important genetic repositories. We suggest that identification of refugia across watersheds and landscapes is needed to better understand reference conditions for woody browse species that may have existed prior to the widespread influences of domestic ungulates and the effects of native ungulates where major predators have been extirpated.

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