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Viewpoint: A theoretical basis for planning woody plant control to maintain species diversity

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Abstract

Range improvement practices have been criticized by scientists and the public because of negative impacts on biodiversity. I present a conceptual model based on ecological theory for designing and planning woody plant control to maintain plant and wildlife species richness and diversity. Broad areas of rangeland have been impacted by overgrazing by livestock and attempted brush control in a manner that has resulted in dense woody plant communities that are resistant to natural disturbances such as fire. State-and-transition models of vegetation dynamics predict these biotic assemblages to be temporally stable and not responsive to successional trends. Cultural energy input in the form of woody plant control is required to change the vegetation configuration of these ecosystems. Anthropogenic input conceptualized and designed based on the intermediate disturbance hypothesis can maximize landscape diversity and may result in a landscape mosaic that supports greater species richness, provides increased forage for livestock, and enhances habitat for many wildlife species. A problem with this approach is that continuing inputs are required to maintain the selected landscape architecture. Development of models to predict the effects of woody plant control patterns on biodiversity will enable range managers to implement management strategies that maintain or increase plant and vertebrate species richness and diversity.

Key Words: edge, intermediate disturbance hypothesis, landscape architecture, species richness, state-and-transition model, succession, wildlife.

Maintaining biodiversity, a multifaceted concept that includes species richness (the number of species in an area) and species diversity (species richness and the degree of numerical similarity among species) (West 1993), is a priority in the scientific community and in public policy (Cairns and Lackey 1992). Maintaining biodiversity is a desirable objective for range and wildlife managers because (1) society values biodiversity and (2) primary productivity in more diverse plant communities is more resistant to perturbations such as drought and recovers more fully following such perturbations (McNaughton 1985, Tilman and Downing 1994).

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Woody plant control is widely applied on western rangelands to increase forage for livestock and to improve habitat for specific wildlife species, such as white-tailed deer (*Odocoileus virginianus* Raf.) and northern bobwhites (*Colinus virginianus* Merr.) (Guthery 1986, Adams et al. 1992, Reynolds et al. 1992). Concern is increasing about the effects of woody plant control and other range improvement practices on species richness and biodiversity (Lewis et al. 1988, West 1993). For example, Fleischner (1994) pointed out that agency management priorities often overemphasize livestock needs at the expense of wildlife. Cooperrider (1991) pointed out that range improvement projects typically emphasize increasing livestock forage and reduce plant and animal species diversity.

My objectives are to review literature on the effects of woody plant control on plant and vertebrate species richness and diversity, and present the argument that ecological theory supports the hypothesis that woody plant control can be applied in a manner that maintains or increases plant and vertebrate species richness and diversity. I present a conceptual model for planning woody plant control to maintain or increase species richness and diversity that aggregates theoretical concepts regarding animal and vegetation responses to disturbance.

A Conceptual Model for Planning Woody Plant Control

Importance of Theory

Management practices should be based on sound theory on which predictions about the outcome of the practices are based (Joyce 1993). A sound theoretical basis is essential to improve the ability of range managers to plan woody plant control to maintain species richness and diversity and to counter arguments that woody plant control is not compatible with maintaining biodiversity. Accepted theories of vegetation function and ecosystem dynamics strongly influence public policy and law, and the efficacy of such policy and law depends upon the soundness of the theory (Johnson and Mayeux 1992).

Effects of Woody Plant Control on Ecological Processes

Effects of woody plant control on plant community composition and ecological processes depend on various factors including the treatment method, composition of the plant community before treatment, soil series, and rainfall before and after treatment. The effects of woody plant control on plant species richness and diversity depend on spatial and temporal scale. For simplicity, my discussion is limited to 2 spatial scales, i.e., landscape versus patch, with the recognition that a heirarchy of patches at several spatial scales can be delineated in many ecosystems. Petraitis et al. (1989) defined a patch as a contiguous area in which the effects of a disturbance are uniform and the subsequent biotic community dynamics are similar. Patches created by woody plant control are, in general, spatially and temporally discrete in contrast to patches created by natural processes (White and Pickett 1985).

Plant species richness and diversity within a patch created by woody plant control may be similar to, lower than, or greater than plant species richness and diversity on nonmanipulated rangeland following treatment. Plant species richness and diversity in ephemeral drainages in the western Rio Grande Plain chained about 40 years earlier or chained (about 40 years earlier) and then root plowed (about 30 years earlier) was similar to nontreated rangeland (Nolte et al. 1994). Forb and shrub species richness and diversity are often temporarily reduced following application of herbicides (Beasom and Scifres 1977).

Effects of woody plant control on vertebrate species richness and diversity within a patch also vary. Gruver and Guthery (1986) found no differences in bird species richness and diversity on rangeland treated with herbicides to control mesquite 12-13 years previously. Nolte (1995) applied Grazon ET+PC (triclopyr and picloram) to 13-ha plots to selectively kill mesquite and cacti (*Opuntia* spp.) without harming other brush species. Bird, small mammal, and plant species richness and diversity did not differ on treated and untreated areas 1 and 2 years posttreatment. Vega and Rappole (1994) examined bird species richness in roller-chopped or disced strips 55–61 m wide that alternated with 244-m-wide nontreated strips in southern Texas thorn woodland. Bird species richness was greater in the nontreated strips than in treated strips. Twenty-three species were captured exclusively in nontreated strips and 2 species were captured exclusively in treated strips. Chaining 16-ha pinyon (*Pinus* spp.) -juniper (*Juniperus* spp.) plots in Colorado reduced bird species richness and diversity but resulted in greater small mammal species richness (Sedgewick and Ryder 1987).

Although woody plant control may reduce species richness and diversity at the patch level, woody plant control may increase species richness and diversity at the landscape scale and increase beta diversity (variation among habitats in the landscape) and landscape mosaic diversity (landscape complexity) (Scheiner 1992) if applied in a mosaic of cleared and untreated patches across a landscape. A landscape that included chained and untreated patches of Ashe juniper (*Juniperous asheii* Buchholz) in central Texas contained lower total bird density but increased richness and diversity (Rollins 1983). Cleared rangeland may support a greater proportion of rodents characteristic of grassland habitats whereas untreated shrubland may support rodent species that prefer woodland habitats (Kruse et al. 1979, Severson 1986). Thus at the landscape scale, a mosaic of smaller, mechanically or chemically manipulated patches interspersed within a woodland matrix may support greater species richness and diversity than homogeneous shrubland or woodland, in part because of differences in adaptations among wildlife species (Smith and Urness 1984).

Brushland is commonly cleared in strips or patches to maintain wildlife populations, particularly game species (Brothers and Ray 1975). The theoretical basis underlying patch or strip clearing is commonly the Principle of Edge. Clearing brush in patches or strips creates ecotones where herbaceous and woody communities abruptly merge. The fundamental concept in the Principle of Edge is that edges may contain organisms that are edge-dependent, in addition to those characteristic of each of the adjacent plant communities, resulting in greater species richness and diversity in ecotones. This increased species richness and diversity is commonly termed "edge effect" (Reese and Ratti 1988).

Although strongly entrenched in wildlife science and application since its conception by Leopold (1933), the edge concept has not been rigorously tested (Guthery and Bingham 1992). Ecosystems are dynamic and the edge concept does not account for temporal changes in vegetation. For example, if a patch within a shrub-dominated ecosystem is cleared of woody vegetation, abrupt edges are created where the remaining shrubs and the herb-dominated community resulting from woody plant control meet. Succession of the herb-dominated community toward shrub dominance proceeds following woody plant control and the edge becomes progressively less abrupt as time passes. If succession proceeds in a manner similar to Clementsian concepts of succession, the 2 communities may ultimately converge in plant species composition resulting in the disappearance of edge.

The edge concept is spatially narrow in that it focuses on ecotones, the transitional boundaries between communities, rather than landscapes. Landscapes may contain a mosaic of patches in various successional stages, in additional to different plant communities resulting from soil heterogeneity and other physical features of the landscape. The edge concept does not explain how biotic diversity may be affected by presence of a mosaic of biotic communities in different stages of succession interspersed across the landscape. In comparison to the Principle of Edge, the intermediate disturbance hypothesis takes into account temporal changes in vegetation and can be conceptualized on a landscape scale.

I propose that the intermediate disturbance hypothesis provides dynamic and robust theoretical underpinnings on which to base woody plant control. According to this model, species richness and diversity within ecosystems are maintained by natural disturbances within patches in the ecosystem (Petraitis et al. 1989). For example, natural disturbances such as periodic fires caused by lightning may burn patches, or stands of shrubs may be killed by frost or by insects. Habitats have maximal species richness and diversity at intermediate levels of disturbance. Level of disturbance is determined by *intensity* and *frequency* of disturbance. I define intensity as severity of disturbance, i.e., the more intense the disturbance the greater the destruction of existing vegetation. Intense disturbances may result in patches that are initially occupied by a few low-successional plant species (Connell 1978). Frequency of disturbance is the number of events per unit time (Petraitis et al. 1989). Frequent intense disturbances will result in the habitat being occupied only by those plant species that mature quickly (Connell 1978).

Woody plant control methods (mechanical, chemical, or pyric) are also disturbance mechanisms that affect species richness and diversity. I will first consider how intensity and frequency of disturbance by woody plant control influence vegetation dynamics at the patch scale, and then expand these concepts to landscape scale. Root plowing is an intense disturbance that creates patches initially occupied by low-successional species (Fig. 1). In south Texas thornscrub discing is a less intense disturbance because few woody plants are killed, resulting in a more species-rich post-

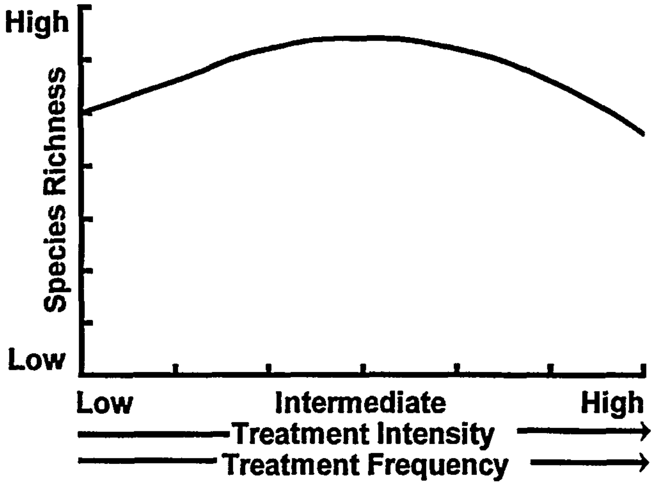

Fig. 1. A conceptual diagram of how frequency and intensity of disturbance by woody plant control might affect species richness at the landscape level, based on the intermediate disturbance hypothesis (modeled after Connell 1978).

treatment plant community because of increased herbaceous species richness and lack of a reduction in woody plant richness and diversity (Bozzo et al. 1992).

As the frequency of disturbances within a patch decreases, plant species richness and diversity increases, at least for a time, because more time is available for the invasion of new species (Connell 1978). Bird species richness and diversity may increase in roller-chopped or disced strips as brush sprouts continue growing (Vega and Rappole 1994). Plant species richness and diversity increased for about 4 years following roller chopping in a longleaf (*Pinus palustris* Mill.) -slash pine (*P. elliottii* Engelm.) forest in north Florida but then declined to pretreatment levels (Lewis et al. 1988).

The increase in plant species richness and diversity stops and begins to decline at some point following disturbances because either the most competitive plants eliminate the rest or the plants most resistant to damage by physical extremes or natural enemies eventually occupy most of the space (Connell 1978). Intermediate frequencies and intensities of disturbance maintain species richness and diversity; however, if disturbances are infrequent species richness and diversity decline.

Expanding these concepts to the landscape scale, intermediate disturbance frequencies and intensities create a broad range of successional habitats (patches), with some recently disturbed, some of intermediate time since disturbance, and some being late successional (Tilman and Pacala 1993). This mosaic of patches at different successional stages allows numerous species to coexist. In contrast, low disturbance frequencies and intensities result in habitats that are almost entirely late successional, whereas with high disturbance frequencies and intensities almost all areas are newly disturbed. Thus, the intermediate disturbance hypothesis provides a theoretical basis for applying woody plant control (mechanical, chemical, or pyric) to create a mosaic of successional habitats to maintain or promote species richness and diversity.

The concept that intermediate disturbances caused by woody plant control may maintain or increase species richness and diversity may be particularly applicable in ecosystems where natural disturbances that impact woody plants, such as fire, have been suppressed. Many shrub communities are so dense because of overgrazing by livestock and failed attempts at brush control (Fulbright 1991) that fire is not a practical tool to reduce brush density. Overgrazing by cattle in certain arid and semiarid landscapes has resulted in severe soil compaction and manipulations such as heavy discing are required to promote infiltration of water and reestablish herbaceous vegetation.

Applying the paradigm that creating a mosaic of different successional stages by woody plant control will benefit or maintain species richness and diversity has several potential pitfalls. For example, although intermediate disturbance may result in greater biotic richness and diversity, in certain habitats application of the model with mechanical woody plant control may result in reduction or elimination of certain species that require large areas of undisturbed habitat. As pointed out by Bailey (1984), not all wildlife species respond similarly to habitat disturbance under all situations. Species that respond positively to disturbance may be gained, whereas species that respond negatively to disturbance may be lost from the landscape.

Further, the vegetation complexity at abrupt edges, such as those created by mechanical woody plant control, attracts passerines but the birds experience greater nest parasitism and predation in edge habitats (Gates and Gysel 1978, Reese and Ratti 1988, Noss and Cooperrider 1994). Reese and Ratti (1988) speculated that predation rates may be high in early successional stages and decline as vegetation complexity increases with age and the contrast at the edge declines.

Another potential problem with basing woody plant control on the intermediate disturbance concept is that continuing cultural inputs are required to maintain a broad range of successional habitats ranging from recently disturbed to late successional. These continuing cultural inputs may or may not be cost-effective, depending on various factors such as method of woody plant control employed. Conner (1985) provided a hypothetical example wherein roller chopping followed by maintenance burning in south Texas was projected to earn a 9.4% rate of return from livestock grazing. The long-term effect of repeated cultural inputs on diversity are not well documented, but they may result in reduced species richness and diversity. Shannon's diversity index values were lower in a shrub community dominated by guajillo (*Acacia berlandieri* Benth.) that was repeatedly shredded at 3-year intervals compared to untreated habitat (Fulbright 1987).

Although woody plant control in patches interspersed in a woodland matrix may increase species richness and diversity, exceptions exist. For example, the areas cleared may be too large or the method applied may severely disturb the existing vegetation. If the method used causes high mortality of existing vegetation, secondary succession following disturbance assumed by the intermediate disturbance hypothesis may not occur. The intermediate disturbance hypothesis is an equilibrium model based on Clementsian concepts of plant succession (Tilman 1994). The concept underlying this model of succession is that a repeatable sequence of seral stages leading to a climax community will occur following disturbance. This model may often not be applicable on semi-arid rangeland.

In arid and semi-arid habitats, vegetation change may not follow repeatable paths as predicted by Clement's model and disturbance may push the system into a new state that is not readily reversed (Friedel 1991). The state-and-transition model is a paradigm that severe disturbance triggers a transition from one state to another, the latter of which may be relatively stable and different in species composition from the original state (Archer 1989, Laycock 1991). A probable example is the species-poor shrub communities that reestablish after root plowing (Fig. 2).

Root plowing upland habitats in south Texas appears to trigger a transition from shrub species-rich mixed brush communities across a threshold to shrub species-poor communities dominated by leguminous shrubs (mesquite and acacias [*Acacia* spp.]). Huisache (*Acacia smallii* Isely) and mesquite (*Prosopis glandulosa* Torr.) composed 95% of the woody plants on rangeland in the Texas Coastal Bend that was root-plowed and raked 14 years earlier, compared to 25% on nontreated rangeland (Mutz et al. 1978). In the Texas Rio Grande Plain, species richness and diversity were 23–35% lower on rangeland root plowed 25–30 years earlier than on nontreated range (Fulbright and Beasom 1987). Nontreated areas in the eastern Rio Grande Plain of Texas contained an average of 19 woody species compared to 7 woody species on areas root-plowed and raked 16–17 years earlier (Ruthven et al. 1993). Species composition of these leguminous shrub communities may remain stable for an indefinite period of time (Fulbright and Beasom 1987, Fulbright and Guthery 1995). Root plowing would be a poor choice as a mechanical method to create an intermediately disturbed landscape if the treatment results in a stable state with low species richness and diversity rather than a lower successional community that will sequentially be replaced by higher-successional communities. Rather than creating a broad range of successional habitats only 2 (disturbed and undisturbed) would be present and the goal of achieving a broad range of successional habitats would not be achieved.

In comparison to root plowing, roller chopping and cabling are less intense disturbances and do not appear to trigger the transition from a mixed brush community to a leguminous shrub community. Following these treatments, vegetation appears to return to a composition similar to the community that existed before treatment (Fulbright and Beasom 1987, Fulbright and Guthery 1995). Shrub species richness and diversity were similar 10 or 16 years after treatment in thornscrub disced once to nontreated thornscrub in southern Texas (Montemayor et al. 1991). Forb species richness was greater during the first year after discing than on nontreated areas in southern Texas (Bozzo et al. 1992). Woody species richness of thornscrub that reestablished following roller chopping or repeated shredding did not differ from untreated rangeland in southern Texas (Fulbright 1987, Fulbright and Beasom 1987). Because woody plant species richness and diversity are not reduced and herbaceous species richness and diversity may temporarily increase, treatments such as discing and roller chopping may result in posttreatment plant communities that are temporarily greater in species richness and diversity than nontreated communities.

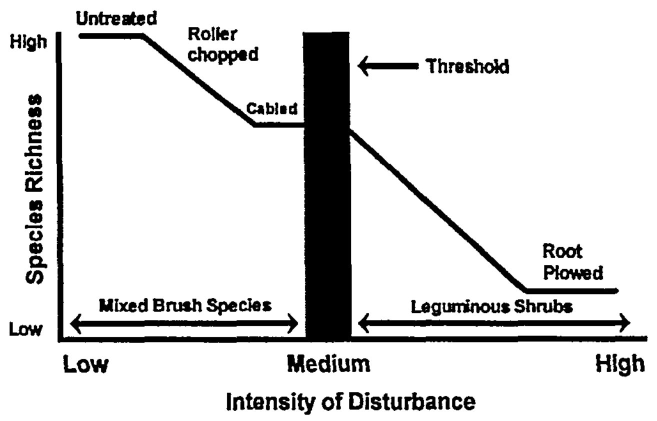

Fig. 2. A conceptual diagram of how different woody plant control practices may operate under state-and-transition models of vegetation dynamics (modeled after Archer 1989). Root plowing may push plant community composition across a threshold resulting in a stable communitiy that does not undergo ecological succession in the traditional sense.

Landscape Architecture to Maximize Landscape and Species Diversity

I propose that woody plant control conceptualized and designed based on the intermediate disturbance hypothesis can increase landscape diversity (Loehle and Wein 1994) and may result in a landscape mosaic that supports greater species richness and diversity, provides increased forage, and enhances habitat for many wildlife species. I am not arguing that woody plant control *should* be used as a tool to increase diversity. Certain scientists argue that natural openings are a more prudent management strategy for maintaining wildlife diversity than maintaining artificial openings (Noss 1991). Rather, I argue that when woody plant control is applied to increase forage for livestock or improve habitat for game that with proper design it can be applied in a manner that also maintains or increases diversity. Applying this concept will require that woody plant control is planned to create a mosaic of intermediately disturbed patches treated at varying intervals of time spatially distributed within a matrix of shrubland. Timing of treatments should be based on rates of succession following treatment so that a variety of communities at varying stages of succession are developed. Additional factors that must be considered in woody plant control planning to increase diversity are size and dimensions of undisturbed habitat required by various plant and vertebrate species; effects of habitat fragmentation and dispersion of fragments; spatial distribution of corridors for movements and interchange among undisturbed portions of the landscape, and corridors to move to and away from disturbed patches; and habitat connectivity requirements of various plant and vertebrate species.

Applying woody plant control in a patches within a matrix of shrubland will result in a large degree of connectivity for shrubland habitats (Fig. 3). Common approaches to clearing patterns that leave shrubland for wildlife habitat are cleared strips that alternate with strips of shrubland or patches of brush in a checkerboard pattern within cleared rangeland. These approaches often result in a paucity of brushy corridors to connect strips or squares of remaining brush.

Cleared patches are essentially habitat "islands" in my model of cleared patches within a shrubland matrix. The size of the cleared patches and the amount of remaining shrubland may largely determine species composition of the patches and species richness at the landscape level. Deciding how large to make the cleared patches and how much shrubland to leave intact will require knowledge of the minimum size of the grassland fragments required to sustain populations of grassland-adapted species and minimum size of the remaining brushland to maintain brushland species. Specialist species require "interior" habitat and may not be sustained if the habitat is too finely fragmented (Lord and Norton 1990). Woody plant control planning to maintain species richness at the landscape level may result in tradeoffs wherein certain "interior" species are eliminated but overall species richness is maintained by the combination of grassland and woodland species.

The appropriate size of cleared patches and amount of remaining shrubland to maintain species richness may vary dramatically in different habitats. For example, Soulé et al. (1992) found that scrub habitat remnants ranging from 10 to 100 ha did not retain all of their native wildlife species for longer than a few decades. Certain species can persist in a region as a metapopulation, even if patch populations are extirpated. However, metapopulation systems are sensitive to changes in rates of immigration and colonization and a system can collapse when immigration rates fall below a certain threshold. Toth et al. (1986) stated that in a mixed forest of Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], areas of individual patches of shrub-seedling-sapling and forested stages should be 5–10 ha and 16–24 ha, respectively, to maintain the majority of wildlife species. Rosenberg and Raphael (1986), also working in Douglas-fir forests, found that stands in the Pacific Northwestern United States <20 ha in size had fewer vertebrate species than larger, continuous forest stands. In contrast, McCoy and Mushinsky (1994) in the Florida scrub found that an archipelago of individually smaller patches supported as many vertebrate taxa as a single large one. Clearly, planning woody plant control to maintain species richness and diversity at the landscape level is extremely complex and development of the appropriate landscape architecture requires the assistance of computer models that consider plant and wildlife diversity in space and time.

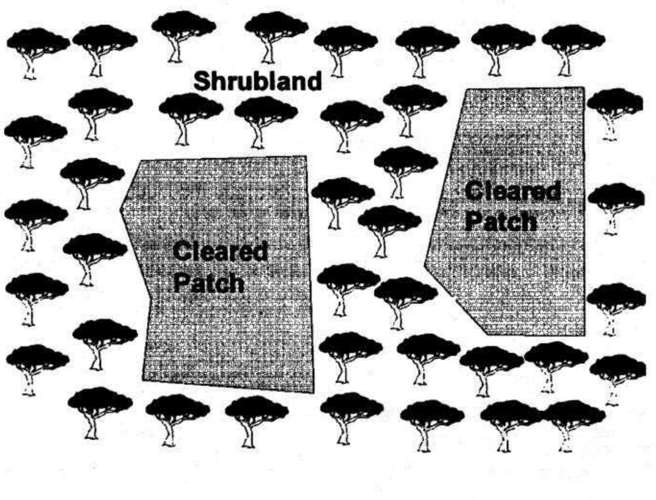

Fig. 3. A hypothetical diagram of how woody plant control might be applied in patches within a shrubland matrix in a manner that maintains or increases plant and vertebrate species diversity.

Models appropriate for maintaining or enhancing vertebrate diversity and wildlife populations have been developed. Hansen et al. (1993) outlined an approach for managing vertebrate species diversity in multiple-use lands at the landscape scale (e.g., 1,000–20,000 ha). Their underlying conceptual model was that animal community response to landscape change can be explained by (1) the suite of life histories represented in a community and (2) the local trajectory of landscape change. Computer models were then used to project abundance for each species under different management regimes. Managers then choose the regime that best meets their objectives. Hof et al. (1994) developed an approach for spatially and temporally optimizing wildlife populations that indirectly models habitat fragmentation and connectivity.

Conclusions and Recommendations

The intermediate disturbance hypothesis may provide a conceptual model on which to plan woody plant control in a manner that maintains or results in an increase in plant and vertebrate species richness and diversity, while increasing forage for livestock and wild ungulates. Effects of woody plant control on species richness and diversity depend on a variety of factors, including the method of woody plant control employed, breadth of treated and untreated patches relative to the requirement of various wildlife species, and the degree of fragmentation of stands of plant communities required by unitype-adapted species. The effects are scale dependent--species richness and diversity may be lower in cleared patches but may be greater in a landscape mosaic consisting of cleared patches interspersed in brushland.

Long-term research in a variety of habitats is needed to test and further refine the conceptual model presented in this paper. Development and validation of computerized models to predict the effects of woody plant control on species richness and diversity in various habitats and to predict the effects of patterns of woody plant control on landscape diversity will enable range managers to plan woody plant control to maintain or maximize biodiversity. The effects of maintaining a landscape mosaic consisting of cleared patches interspersed in a martrix of brushland on ecosystem productivity and resilience also warrant investigation.

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