

# Patch structure, dynamics and implications for the functioning of arid ecosystems

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Plant cover in ecosystems that are strongly water-limited is not continuous and is usually less than 60%. Therefore, it is reasonable to ask whether the distribution of plant cover is homogeneous, random or clumpy. A recent review of the structure of arid ecosystems throughout the world, supports the idea that vegetation is commonly arranged in a two-phase mosaic composed of patches with high plant cover interspersed in a low-cover matrix<sup>1</sup>. References to patchy distributions of plant cover started in the late 1950s (Refs 2–5) when Greig-Smith<sup>6,7</sup>, among others, studied plant population patterns in Africa. Earlier, Watt<sup>8</sup> proposed a model for the dynamics of patches that was a milestone in community ecology. He reviewed evidence from mesic regions – but not from arid ecosystems – and proposed that plant communities were composed of different patch types, each one at a different successional stage. Since then, there have been many studies of patch dynamics in mesic forests and grasslands<sup>9</sup>. However, synthetic studies of patch dynamics in arid and semiarid environments have been comparatively scarce. Recent papers have shed light on the commonalities of the dynamics of the two-phase mosaic in arid ecosystems, with key implications for ecosystem functioning and management of arid lands.

## The patterns: tiger versus leopard

Vegetation patterns in arid ecosystems are characterized by the size, shape and spatial distribution of high plant-cover patches. Low-cover patches are usually considered as a matrix, in which denser patches are distributed. In some ecosystems, the dense patches form bands or stripes and communities presenting this pattern are generically named as banded or 'tiger' vegetation<sup>10</sup>. In other ecosystems, the dense vegetation patches are irregular in shape; following the above analogy, here they are referred to as spotted or 'leopard' vegetation (Fig. 1).

Banded vegetation has been described in arid ecosystems in North America<sup>11,12</sup>, Africa<sup>3,5</sup> and Australia<sup>13–15</sup> (Table 1). In banded vegetation, dense patches represent approximately 20% of the area, whereas the rest of the area is dominated by bare soil with sparse vegetation. Bands are formed by clumps of plants that extend mainly along an axis perpendicular to the slope; their dimensions range

**Arid ecosystems present a two-phase mosaic structure of high- and low-cover patches. Vegetation patches differ among ecosystems in size and shape. However, recent studies indicate striking similarities in patch dynamics and in mechanisms explaining their origin and maintenance. Two major types of system, banded and spotted vegetation, which are characterized by patch shape, both originate from common mechanisms, although each is dominated by a different driver. Banded vegetation occurs when water is the dominant driver of the redistribution of materials and propagules, whereas spotted vegetation results when wind is the major redistribution driver. Model analysis indicates that patchy vegetation structure enhances primary production.**

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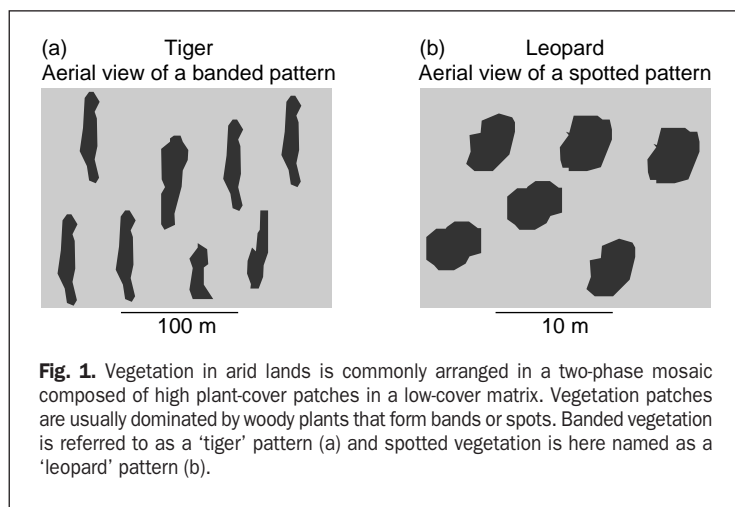
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from 5–50 m in width and from 20–400 m in length (Fig. 1a). Four units comprise the banded pattern: the interband area, the front or band upslope, the main band body, and the band downslope<sup>14,16</sup>. Bare ground dominates the interband area, although annual herbs, sparse perennial grasses or woody plants can be present. In the front area, total cover is high and is usually dominated by tussock-forming grasses. In the body area, total cover is also high, but woody plants appear to be the conspicuous component of vegetation. Tussock grasses can be present, as in the Mexican Chihuahuan desert<sup>12</sup>, or absent, as in the Central Australian desert woodland<sup>13</sup>. Finally, downslope areas are characterized by low total plant-cover and tree corpses. In most cases, different topography and soil characteristics are associated with different vegetation phases<sup>15</sup>. For example, in Eastern Australia, the interband area had a steeper slope

than the front and body areas, whereas the downslope area was located in a step or drop compared with that of the body area<sup>14</sup>. Soils have a high nitrogen and carbon content in the vegetated units, particularly in the upper soil layers<sup>14</sup>.

Spotted or leopard vegetation has been reported for several regions in North and South America (Table 1). High-cover patches or spots are isodiametric or have irregular circular shapes. Vegetation spots, which are more variable in size than bands, range from 1 m to less than 100 m in diameter (Fig. 1b). A recent study reported that in the Patagonian steppe, the high-cover patch type is formed by a shrub encircled by a dense and tight ring of tussock grasses<sup>17</sup>. The shrub-ring patch-type is approximately 1 m in diameter, and accounts for only 18% of the entire community cover. In northern Patagonia, vegetation patches are located in small areas that are at a slightly higher topographical level and have higher nutrient availability than the low-cover phase<sup>18</sup>. In the Chilean Matorral, vegetation is organized in clumps composed mostly of shrubs; it is very unusual to find solitary individuals<sup>19,20</sup>. Shrub seedlings are absent in the interclump area except for those of a weedy shrub (*Baccharis* spp.). Clumps located in pole-facing slopes (moist and cool) are larger (65 m in diameter) than those located in valley bottoms (19 m in diameter) or equator-facing slopes (7 m in diameter). In the Sonoran desert (southern United States and northern Mexico), the



**Fig. 1.** Vegetation in arid lands is commonly arranged in a two-phase mosaic composed of high plant-cover patches in a low-cover matrix. Vegetation patches are usually dominated by woody plants that form bands or spots. Banded vegetation is referred to as a 'tiger' pattern (a) and spotted vegetation is here named as a 'leopard' pattern (b).

columnar saguaro cactus *Carnegie gigantea* dominates the vegetation<sup>21</sup>. Young saguaro plants are located beneath desert trees and shrubs, such as palo verde (*Cercidium microphyllum*), mesquite (*Prosopis juliflora*) or creosote bush (*Larrea tridentata*)<sup>22</sup>. This spatial distribution determines a two-phase mosaic, with saguaro plants constrained to the woody plant patches.

**Patterns and processes in two-phase mosaics**

The two-phase mosaic affects the rates of several ecosystem processes, from water dynamics and nutrient cycling to biotic interactions (Table 2). Water dynamics are different in the two phases. In tiger ecosystems, interband areas represent areas of catchment and transport of rainfall water downslope, whereas vegetation bands are sinks for the transported water. Water movement occurs because of the gentle slope and the low infiltration characteristics of the interband area. Vegetation in the band reduces water velocity and increases infiltration<sup>11,13,23,24</sup>. In leopard vegetation, water infiltration is higher and soil evaporation is lower in the densely vegetated patches compared with that in the bare-soil dominated matrix<sup>18,25</sup>.

Nutrient dynamics are also different in the two phases. In arid ecosystems, it is common to find islands of fertility associated with individual plants (shrubs and tussock grasses)<sup>26,27</sup>. Both banded and spotted vegetation display a

pattern of higher soil organic matter and mineral nutrients in the vegetation patches compared with the low-cover matrix<sup>18,26,28</sup>. As a recent review indicates, islands of fertility are the consequence of accumulation processes driven by abiotic and biotic processes<sup>27</sup>. Abiotic processes, mainly driven by wind and water, include redistribution of fine soil particles, associated mineral nutrients and litter that is concentrated underneath vegetated patches. Biotically driven accumulation results from the action of roots, which absorb nutrients from the soil under the densely vegetated patches, as well as from the soil of the bare-soil matrix. Whereas mineral nutrients are absorbed from both types of patches, above-ground litter falls mostly in the vegetated patches, enriching these patches with biotically important mineral nutrients.

Recent studies of the recruitment of new individuals in the low- and high-cover patches indicate that in banded and spotted communities there are differences in the intensity of ecological interactions (such as competition, facilitation, seed and seedling predation) or rates of processes (such as primary and secondary dispersal). Seeds tend to accumulate near vegetation patches, and have low density in bare-soil areas (both the interband and interspot areas). Although, in some cases, the seed rain is uniform, abiotic redistribution and differential predation generally results in a higher concentration of seeds underneath, or close to, vegetated patches. In banded vegetation, water is the main agent of seed dispersal, whereas in spotted vegetation, wind and animal action are the major dispersal agents<sup>20,29-31</sup>. Birds, perching in trees or shrubs, promote a concentration of seeds equivalent to the accumulation resulting from water run-off and wind. Adult plants, in bands and spots, increase seedling survival by ameliorating the microenvironment or by deterring herbivory<sup>19,32,33</sup>. In other developmental stages, adult plants can reduce seedling survival by decreasing light or water availability<sup>21,29,34</sup>. Together, these studies suggest that the origin and maintenance of both bands and spots are the result of the subtle balance between competition and facilitation (between seedlings and adult plants), with each phenomenon dominating the development of the two-phase mosaic at different times. Indeed, conditions are more favorable in ecotones or transient microsites, in which seeds are abundant and facilitation temporarily overshadows competition by adult individuals. For example, in the

**Table 1. Sites in different continents where vegetation is composed of a two-phase (high-low plant cover) mosaic**

Continent	Precipitation (mm year <sup>-1</sup> )	Pattern	Size (m) <sup>a</sup>		Dominant life form in high-cover patches	Refs
			Width	Length		
<b>Australia</b>						
Alice Spring (Central Australia)	250	Bands	25	200	Trees, perennial grasses and herbs	13
Lake Mere (Eastern Australia)	290	Bands	20	1000	Trees and perennial grasses	14,15
<b>Africa</b>						
Burao (Somalia)	200	Bands	50	500	Trees, perennial grasses and herbs	5
Jebel Mandara (Sudan)	250	Bands	100	no data	Trees and perennial grasses	3
<b>North America</b>						
Chihuahuan desert (Mexico)	264	Bands	45	250	Trees, shrubs and perennial grasses	12,29
Saguaro National Park (USA)	250	Spots		<8	Trees and succulents	20
<b>South America</b>						
Río Mayo (Argentina)	160	Spots		<1	Shrubs and perennial grasses	17
Puerto Madryn (Argentina)	188	Spots		<2	Shrubs and perennial grasses	28,46
Los Dominicos (Chile)	450	Spots		20-60	Shrubs	19,20

<sup>a</sup>Bands are characterized by width and length, and spots by diameter (given in length column).

Patagonian steppe, conditions for seedling establishment are most favorable around shrubs when the ring of grasses is not yet complete<sup>30</sup>. Similarly, recruitment is at a maximum in the upslope ecotone between vegetated bands and bare-soil areas<sup>29</sup>.

**Patch dynamics in banded and spotted vegetation.**

Conceptual models of patch dynamics in banded and spotted vegetation infer spatio-temporal relationships from current structure and recruitment dynamics (Box 1). In general, patch dynamics include both a building and a degenerative phase (i.e. the upgrading and downgrading phases of Watt<sup>8</sup>; Box 1a). In both tiger and leopard patterns, the building phase starts with the establishment and growth of woody plants in a certain location. As woody plants grow, the microenvironment in the neighborhood changes (e.g. higher water infiltration, reduction in radiation reaching the soil, and accumulation of seeds, fine soil particles, litter and other plant debris) promoting the establishment of vegetation and consequently, building the patch. The degenerative phase starts with the death of the dominant individuals. Plant cover decreases, which in turn leads to wind- and water-induced degradation of the fine-particle soil mound that was associated with the patches. As a result, the microenvironment is no longer favorable for seedling establishment<sup>12,17,29</sup>.

From a landscape perspective, tiger and leopard patterns differ in their dynamics. In banded vegetation, the bands 'climb' the slope as new individuals establish in the front, and old individuals die in the downslope border<sup>29</sup>. In spotted vegetation, each patch in the mosaic has its own dynamics and there is no unidirectional overall landscape pattern.

Pickett and White<sup>9</sup> concluded that disturbance was the major driver of patch dynamics in mesic ecosystems and that disturbance originates in a wide range of exogenous (e.g. fire) and endogenous (e.g. death of canopy individuals) causes. On the contrary, in arid ecosystems with tiger and leopard patterns, endogenous causes predominate (Box 1).

**Origin and maintenance of tiger and leopard vegetation**

Tiger and leopard vegetation might be the result of the same general mechanism inherent in these two-phase patterns. Differences in the relative importance of the drivers determine the occurrence of one pattern or the other. The basic mechanism is a redistribution of water, nutrients and seeds (resulting from the presence of dominant woody plants), which creates and maintains dense vegetation patches. Water is the major agent of

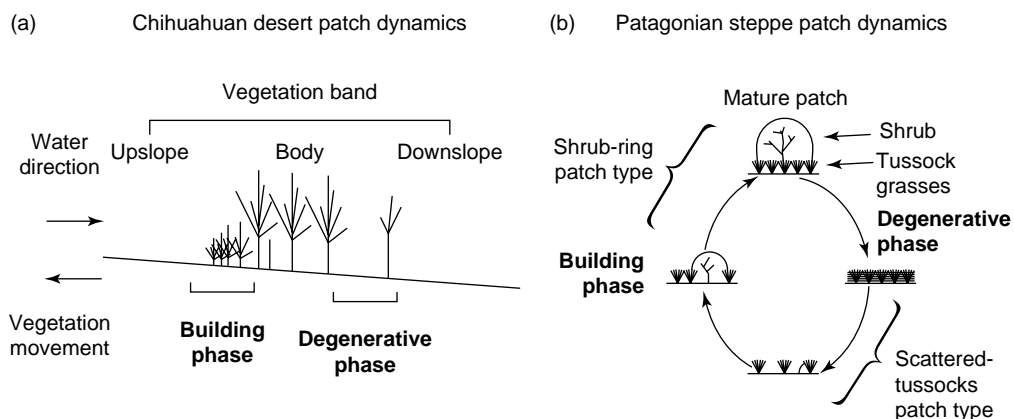
**Table 2. Reported processes with different rates in the two phases of banded and spotted ecosystems**

Process	High-cover patches	Low-cover matrix	Refs
<b>Abiotic processes</b>			
Infiltration	High	Low	11,13,23,24
Run-off	Low	High	11,13,18,23,24
Bare soil evaporation	Low	High	11,23,25
Wind and water erosion	Low	High	18,27
Deposition of fine materials	High	Low	18,26,27
<b>Biotic processes</b>			
Competition	High	Low	29,30,32,34
Facilitation	High	Low	20,30,32,34
Herbivory	High?	Low?	40-42
Secondary seed dispersal (range)	Short	Long	19,20,29,31
Transpiration	High	Low	29,34
N mineralization	High	Low	14,28,39,47

redistribution in tiger vegetation, whereas wind and animals are the major cause of redistribution in leopard vegetation. Moreover, in tiger patterns, water is the main driver of secondary seed dispersal, whereas in leopard patterns, wind or animals are the main agents of dispersal. Water flows predominantly in one direction, and consequently seeds accumulate only in the upslope portion of the bands and seedlings are constrained to that position<sup>12,29</sup>. Wind and animals, however, do not accumulate material and

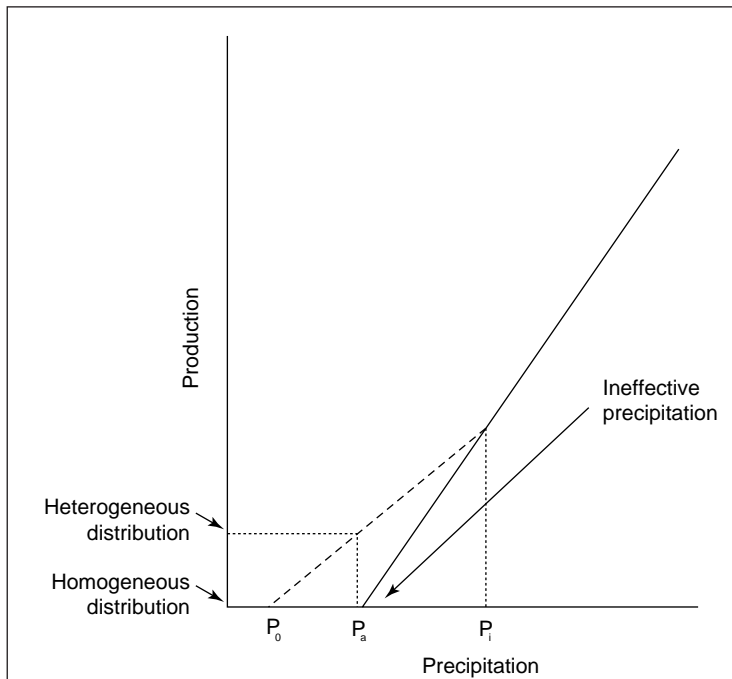
**Box 1. Patch dynamics in tiger and leopard patterns**

Patch dynamics in both tiger and leopard patterns (Fig. 1) are associated with growth and mortality of woody plants. The Chihuahuan desert is an example of banded vegetation (a); in this ecosystem, most recruitment of shrubs and trees occurs in the upslope of the band. Mature individuals are located in the body of the band, whereas dying individuals are downslope of the band. Active growth (building phase) occurs in the upslope front of the band, where most of the seeds transported by run-off water is collected, and where the balance between competition and facilitation is more favorable for young plants. Downslope, mortality is the dominant process because most run-on water has infiltrated upslope and most nutrients have been sequestered in the front and the body of the bands (degenerative phase)<sup>13,16,29</sup>. The result of these vegetation dynamics is that bands 'climb' the slope as recruitment occurs in the upslope shifting-ecotone of the bands and mortality occurs mostly in the downslope border.



(Online: Fig 1)

In the spotted vegetation of the Patagonian steppe (b), the model that relates the two patch types of the mosaic indicates that establishment of a shrub can occur in any location in the low-cover matrix. As the shrub grows (building phase), it creates a neighborhood with aerial protection that promotes both seed accumulation and seedling establishment, resulting in the formation of a ring of tussock grasses. As the ring of grasses is completed, competition between the grasses overshadows facilitation by the shrub, and establishment of grass seedlings decreases<sup>30</sup>. When the shrub dies and begins to collapse (degenerative phase), aerial protection disappears and below-ground competition dominates over any facilitation effects. Therefore, mortality of grasses increases, leading to a thinning of the ring of grasses. Tussock mortality slows down as grass density reaches values equivalent to that of the matrix; the ring then loses both its identity and the remnant grass individuals form the scattered-tussock patch type<sup>17</sup>.



**Fig. 2.** Hypothetical relationship between mean annual precipitation and production for arid and semiarid ecosystems (unbroken line). In ecosystems with a homogeneous distribution of plant individuals, which receive precipitation equal to  $P_a$ , production will be zero because it is below the production threshold (i.e. ineffective precipitation)<sup>35</sup>. In ecosystems with a heterogeneous distribution of individuals, another function relates production with precipitation (dashed line). The low-cover matrix (source patches) will lose water, causing a shift in status from  $P_a$  to  $P_0$  without changing their production, which is already zero. High-cover patches (sink patches) will have a higher water availability,  $P_i$ , resulting from the water that falls directly on them in addition to the run-on. If water availability is equal to  $P_i$ , production will be higher than zero and therefore production in heterogeneous ecosystems will be higher (modified from Refs 1 and 36).

seeds only on one side<sup>17,31</sup>. Animal activity is not unidirectional and wind, although it can in some cases have a predominant direction, is more variable than the effect of slope on water movement, and has similar effects windward and leeward (as a result of direct push and suction).

**Implications for the functioning of arid ecosystems**

The concentration of resources into patches might result in an overall increase in production and diversity<sup>1,35,36</sup>. Several empirical studies show that the relationship between annual precipitation (between 250 and 1300 mm) and production is described by a straight line with a slope lower than one and a negative y intercept<sup>37</sup> (Fig. 2). A negative y intercept means that the straight line intercepts the x axis at a value of precipitation greater than zero. In ecological terms, this indicates that there is a precipitation threshold below which there is no production. Noy-Meir<sup>35</sup> named this parameter the ‘ineffective precipitation’ or ‘zero-yield’ intercept. In a homogeneous ecosystem, production will be zero if precipitation is below the ineffective precipitation. In a heterogeneous ecosystem, water redistribution determines a new resource status for both phases of mosaic ecosystems in which the low-cover matrix (source patches) releases water to high-cover patches (sink patches). Consequently, low-cover patches become drier and poorer, whereas vegetated patches become wetter and richer. The redistribution of resources between sources and sinks results in an increase in total production. Sink patches, which received input from the source patches, are now above the resource threshold and have a production greater than zero. Source patches have lost resources, but

their production has not changed and is still zero. From this analysis it follows that overall production will be higher in a heterogeneous system compared with that in a homogeneous system (Fig. 2). The difference in production between homogeneous and patchy systems depends on the proportion of incoming water that runs off, and on the relative abundance of sinks, which, in the model, determines the slope of the dotted line. Results from a simulation model, which calculates production from a spatially explicit design of the landscape, confirmed this hypothesis for banded vegetation<sup>24</sup>. These results also indicated that the proportion of the two types of patch (source and sink) that maximizes production, varies with annual precipitation.

Nutrient distribution is also heterogeneous in a two-phase mosaic and similarly, it can result in a promotion of production. Invoking a mechanism similar to water redistribution, we suggest that islands of fertility, underneath the vegetated patches, are sinks for nutrients exported from the low-cover matrix<sup>27</sup>.

The spatial heterogeneity resulting from tiger or leopard vegetation, enhances  $\alpha$  and  $\beta$  diversity<sup>38,39</sup>. Vegetated patches and their dominant woody plants serve as protection from grazing for preferred plant species and protection from predation for small animals<sup>40,41</sup>. The contrasting environmental conditions of vegetated patches and the low-cover matrix, selects for different characteristics for species and ecotypes<sup>42</sup>.

**Tiger and leopard: management implications**

Current scenarios of global change include a combination of changes in land use, and climate and atmospheric composition<sup>43</sup>. Sound management under these scenarios should consider changes in patch structure and their effects on ecosystem functioning. Changes in climate and land use could modify the relative importance of water, wind and animals as redistribution vehicles. In turn, these changes might result in large changes in vegetation pattern and physiognomy and therefore, changes in ecosystem functioning. The global-change effects on vegetation pattern could have cascading effects, resulting in an acceleration of global change. For example, in regions where climate change increases precipitation amount or intensity, water run-off will increase and might result in a shift from leopard to tiger patterns. In banded vegetation, however, an increase in precipitation intensity might augment run-off to a point that exceeds the capacity of sink bands. The excess run-off could erode the bands and consequently, create a pattern on a coarser scale.

A pervasive pattern of land-use change in arid ecosystems is the alteration of grazing intensity. Grazing patterns can be finer or coarser than vegetation patterns and therefore, can erase or generate patterns<sup>44</sup>. Examples from both banded and spotted ecosystems indicate that an increase in grazing intensity could change the grain of the pattern<sup>14,45–47</sup>. Grazing and trampling compact the soil in the interpatch area, reduce water infiltration and increase water run-off<sup>24</sup>. Reduction in plant cover in vegetated patches might increase evaporation over transpiration while reducing aerial protection for the plants underneath. These changes might first shift vegetation patterns from tiger to leopard, and then lead to a completely different system with a much coarser grain, and probably a lower productivity.

Pioneering techniques for recovering degraded arid lands are already taking into account the importance of the two-phase structure for the functioning of arid ecosystems. These techniques include practices that foster the source–sink dynamics in those situations where it has been

damaged. Australian efforts have focused on restoring the two-phase functioning (by adding woody debris to alter the water balance) rather than on rebuilding the structure (by planting or seeding plants). The results, after three years, are encouraging given that both soil properties and vegetation cover have shown significant recovery<sup>48,49</sup>.

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