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Linking diverse terminology to vegetation type-conversion, a complex emergent property

ABSTRACT

Ecosystems worldwide are facing complex interacting stressors that are leading to rapid and potentially irreversible change. Many of these changes involve vegetation type-conversion in various stages and forms. A variety of terms are applied to changes in ecosystems around the world to describe some aspect of long-lasting changes in plant communities. Here we evaluate a representative list of analogous terms for processes and patterns involved in vegetation type-conversion, highlighting similarities and differences. The list illustrates a common problem in ecology, *viz*. how similar terminology may actually describe different aspects of complex processes. Linking this terminology under a unified, umbrella concept of vegetation type conversion and placing it into the context of an ecological resilience framework, including community reorganization, may help resolve research agendas and conservation efforts.

INTRODUCTION

Rapid and widespread changes in vegetation communities are an emerging global conservation problem (e.g., Syphard et al. 2018, Keeley et al. 2019). The term “vegetation type-conversion” (VTC) has long been used by ecologists to describe this problem (e.g., in California shrublands, Bentley 1967, Countryman 1974, Haidinger and Keeley 1993, Keeley 2002, Syphard et al. 2006) because the component processes of VTC have been observed across a wide range of ecosystems and contexts. For example, studies have addressed conversion of chaparral to grassland in southern California (Syphard et al. 2018), transformation of fynbos to closed, invasive *Pinus* spp. forests in South Africa (Richardson and Rejmánek 2011), and the widespread conversion of forest to shrubland or grassland throughout the interior West and Rocky Mountains of the USA (Liang et al. 2017, Barton and Poulos 2018, Guiterman et al. 2018, Walker et al. 2018). There is also the loss of ancient, open savannas to afforestation in Madagascar, as well as in places like the southeastern USA (Bond 2019).

This widespread change in disparate communities and ecological contexts has been described using diverse terminology in the ecological literature. A variety of descriptors for processes involving vegetation type-conversion’ have been used to describe abrupt and persistent change in vegetation communities, many of which are driven directly or indirectly by human activity. As a result, independent observations of VTC occurrence have spawned a wide range of valuable, but potentially competing, terminologies. To highlight similarities and differences among this terminology, we have compiled a range of terms used in the ecological literature to describe the variety of processes and outcomes of VTC (Table 1). We do not presume this list to be exhaustive, but rather representative of the range of terminologies in use, and the varying focus on different aspects of this large and complex process. Some terms are specifically useful for describing VTC in specific ecosystems and associated processes but may not generalize to research and management efforts in other systems. Many of these are also useful at particular spatial and temporal scales and biological levels of organization; some focus on particular mechanisms, while others describe VTC as an emergent outcome of multiple processes (Hodges 2008, van Nes et al. 2016).

LINKING DIVERSE TERMINOLOGY

A degree of dynamic change is, of course, fundamental to the contemporary understanding of ecosystems (Pickett and White 1985, Botkin 1990, Pausas and Bond 2018, Bond 2019). Thus, a particular challenge in studying VTC is to distinguish it from the background of ecological dynamics that has characterized the history of life on Earth. One common theme in studies of abrupt change is that VTC is typically caused by one or more drivers (e.g., climate change, invasive species, pollution, process perturbations, habitat fragmentation or loss) that exceeds natural variability (Table 1). These drivers are often anthropogenic and difficult to reverse, operating at various chronological and spatial scales that are difficult to discern (e.g., Cooper 1922, Beisner et al. 2003, Inderjit et al. 2017).

A second common theme among most studies is that while the process of VTC may start out small, incremental, and difficult to detect, community assembly processes, species interactions, modified disturbance regimes and shifts within and among plant functional types can lead to persistent community change. These changes may ultimately reach an irreversible tipping point (e.g., Scheffer et al. 2009a, van de Leemput et al. 2014, van Nes et al. 2016, Jacobsen and Pratt 2018), leading toward an alternate or novel metastable state, unless there is a timely reprieve from the particular driver(s) in play. Moreover, even when the original driver is relaxed, the system is likely to follow a hysteretic pathway, i.e. following a novel recovery trajectory and not simply recapitulating the degradation path (Petrone et al. 2007, Suding and Hobbs 2009, Suding et al. 2016). The proximate endpoint of VTC is a change in composition or dominance of the vegetation community at some meaningful spatial and temporal scale (e.g., Beisner et al. 2003, Inderjit et al. 2017, Rocha et al. 2018, Falk et al. 2019). There may also be a permanently changed disturbance regime that reinforces these changes (Falk 2013, Pausas and Keeley 2014, Keeley and Pausas 2019, Miller et al. 2019)

VTC IN THE RESILIENCE FRAMEWORK:

The emerging ecological resilience paradigm provides a complete framework in which to contextualize VTC as an endpoint of successive changes in an ecosystem (Falk et al. 2019). Resilience responses vary across scales of time, space, and biological organization. Initially, individuals may *resist* perturbations or stressors, allowing them to persist in the community. Once resistance has been overcome by the drivers and mortality becomes widespread, populations must *recover* by a different array of mechanisms involving establishment of new individuals. If recovery is incomplete or compromised (e.g., Davis et al. 2019, Keeley et al. 2019), communities may *reorganize* into alternative states, which may be transient or persistent. Thus, VTC is an emergent response in which a community reorganizes as the endpoint of processes in which individuals can no longer resist, and populations can no longer recover. That is, VTC is the equivalent of community reorganization within the resilience framework (Falk et al. 2019).

The ubiquity of the drivers of VTC (e.g., climate change, invasive species/disease, pollution, process perturbations/aka altered disturbance regimes, and habitat fragmentation/loss) suggests that in some instances conservation for a resilient metastable state may be a more realistic goal than restoration to the reference ecosystem state for some ecosystems (Beisner et al. 2003, Higgs et al. 2014, Falk 2017, Inderjit et al. 2017, Rocha et al. 2018). For example, under current and expected future fire regimes, the conversion of some conifer forests to oak woodlands may be unavoidable and provide for a stable assemblage of native species with associated ecosystem services (Holling 1973, Standish et al. 2007, Keeley et al. 2019, Miller et al. 2019). This change in perspective may be necessary for managers tasked to conserve ecosystem resilience where conditions are driving vegetation towards novel metastable states (Guiterman et al. 2018, Higuera et al. 2019, Miller et al. 2019). Under current and emerging environmental conditions, the changed state may be more resilient than the historical state so there should be limited expectations to restore the historic, reference type-ecosystem. In contrast, there are numerous examples of VTC involving invasive non-native grasses where the alternate state is considered ecologically and societally undesirable (Brooks et al. 2004, Stevens and Falk 2009, Rowland et al. 2010, Keeley et al. 2011, Marshall et al. 2012, Olsson et al. 2012, Chambers 2014). In these cases, where the reorganized community is considered unacceptable (e.g., increased flammability and watershed degradation following the replacement of southern California shrublands with non-native annual grasses), they may require increased management attention.

In other circumstances, however, type-converted systems may represent outcomes that provide at least some conservation benefits and ecosystem services under altered environmental and climatic conditions. Some conversions involving replacement by other native species, for example, may be more tolerable from a conservation perspective. Guiterman et al. (2018) documented persistent replacement of ponderosa pine (*Pinus ponderosa* var. *scopulorum*) and dry mixed-conifer forest by extensive stands of Gambel oak (*Quercus gambellii* Liebm.), a drought- and fire tolerant native shrub that provides soil stabilization and wildlife habitat. Type conversions must be evaluated from multiple perspectives, including key ecosystem services such as carbon sequestration (Zhang et al. 2015). Similarly, the increasing use of assisted migration and related strategies rests on the premise that modifications of existing species distributions may in some cases provide important conservation value (McLachlan et al. 2007, Vitt et al. 2010, Hernández-Castellano et al. 2020, Lundgren et al. 2020).

CONCLUSION

VTC may be usefully conceived as a complex, emergent community response to multiple stressors, in which various community properties are at different stages along the resilience pathway. Once a VTC threshold has been crossed, it will represent a changed end state that may hold conservation value in some cases but not others (Holling 1973, Peters et al. 2004, Suding and Hobbs 2009, Falk et al. 2019). Linking analogous concepts and terms helps to form a broad perspective from which to evaluate community reorganization. This perspective may facilitate more regional and global collaboration toward managing or accepting the inevitable changes in the Anthropocene.

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Table 1: Examples of vegetation type conversion terminology.

Analogous Term	Summary of the Term	Citation
Abrupt climate-independent fire regime change	Within the climate envelope, some non-climate "drivers" (i.e., fauna, invasive plants, or socioeconomic factors) "alter community composition in ways that set the community on a trajectory of more lasting changes."	(Pausas and Keeley 2014)
Abrupt ecological change	Within the climate envelope, some "trigger" disturbance causes a "rapid reorganization of ecosystem mass and energy threshold response in key biotic and abiotic ecosystem components".	(Falk 2013)
Abrupt ecosystem transition	A change in vegetation occurring for low elevation ponderosa pine and Douglas-fir forests with climate change (indicated by vapor pressure deficits, higher surface temperatures, and lower soil moisture) combined with high severity fire.	(Davis et al. 2019)
Alternations	Change from a chaparral climax community to another, depending on the moisture conditions and fire frequency. In wet, mesophytic forests, chaparral has "transgressed" its normal climate limits due to repeated fire, invading conifer	(Cooper 1922)

	forests, whereas in xerophytic communities, chaparral is “pushed-back” by grasses.	
Alternative Stable Equilibria	Where “distinct equilibrial states are locally stable”, making long-term outcomes unpredictable for dynamic systems. In general, the outcomes depend “on both initial conditions and fire stochasticity”.	(Miller et al. 2019)
Alternative Stable States	“From the modeling perspective, alternative stable states might arise through state variables or parameter shifts” Two ways it can happen: either the environment or the community changes, to affect the other reciprocally. Community can be altered directly, or via perturbations.	(Beisner et al. 2003)
Cascading regime shift	This occurs via the driver sharing, domino effects, and hidden feedbacks of interacting regime shifts.	(Rocha et al. 2018)
Catastrophic events leading to ecological surprise	This is ecosystem change resulting from “characteristic nonlinear behaviors that are often generated by cross-scale interactions and feedbacks among system elements”	(Peters et al. 2004)
Collapse state	An abrupt change in ecosystem state that is irreversible, widespread, and undesirable due to the loss of ecosystem services and biodiversity.	(Lindenmayer et al. 2016)
Community reorganization	“Human driven vegetation change can occur through: non-native species introductions; population outbreaks or collapses; range expansions or contractions; and range shifts of both native and non-native species.” Resulting from drivers that also vary in time and space.	(Inderjit et al. 2017)
Composition shift	“[Changes] in forest structure [dbh, composition, and water balance] between historical (1930s) and contemporary 2000s) surveys”.	(McIntyre et al. 2015)
Critical slowing down	This is an earlier stage in the change process, but one that indicates an impending tipping point or “critical transition” to a new state. Early warning time series signs include 1) slower recovery from perturbation, 2) increased autocorrelation of the system, and 3) increased variance. Early warning spatial patterns are (eco)system specific.	(Scheffer et al. 2009b, van de Leemput et al. 2014)
Degradation without recovery	This is a description of rangelands that are “degraded due to overuse” and where “soil carbon is lost to the atmosphere.”	(Havstad et al. 2007)

Ecological conversions	Changes in species distributions (i.e., novel configurations) in response to a combination of changing climate and severe disturbance triggers.	(Falk 2013)
Ecological drought	This refers to droughts that lead to water deficits that drive ecosystems beyond thresholds of vulnerability, impair ecosystem services, and trigger feedbacks in natural and human systems.	(Crausbay et al. 2017, Jacobsen and Pratt 2018)
Ecological transformation	This occurs when resilience is exhausted, serious thresholds are crossed, and valuable ecosystem services are lost.	(Millar and Stephenson 2015)
Ecosystem transformation	An ecosystem shift (i.e., change in both vegetation and function), in this case resulting from relaxed herbivore pressure and increased landscape-scale fire at the end of the Pleistocene in Australia.	(Rule et al. 2012)
Ecosystem transformation	"As humans have become more abundant, we have transformed large parts of the Earth's surface from their pre-human 'natural' state into entirely different landscapes and seascapes."	(Barnosky et al. 2014) see pp.92-93
Erosion of Ecological Memory	The loss of the "adaptations, individuals, and materials that persist after a disturbance and shape responses to future disturbance" (i.e., loss of information legacies and materials represents the loss of ecological memory).	(Johnstone et al. 2016)
Extinction dynamics	A population biology concept encompassing synergistic drivers (i.e., amplifying feedbacks) toward extinction given global climate change.	(Brook et al. 2008, Ceballos et al. 2017)
Forest simplification	This is forest composition change in the form of reduced tree species richness in tandem with diminished "landscape-level C sequestration potential".	(Liang et al. 2017)
Functional type-conversion	Functional type-conversion is indicated by the loss of certain functional groups within an ecosystem. For example, killing a large proportion of relatively shallow-rooted, obligate seeding shrub species, leaving only resprouting shrub specie.	(Jacobsen and Pratt 2018)
Interval Squeeze	Occurs when reduced fire return intervals "squeeze" an already drought-reduced	(Enright et al. 2015)

	demographic envelope, causing extinctions and altering the community composition.	
Novel assemblage	The redistribution of species into new biotic associations in response to environmental change.	(Hobbs et al. 2018)
Novel ecosystem states	The result of "grass invasions and climate change [acting] in concert to induce land degradation".	(Yu et al. 2016)
Novel ecosystems	These have less than 70% of habitats that were present 500 years ago and more than 5 people per Km^2.	(Mittermeier et al. 2003, Barnosky et al. 2017)
Reorganization	The community-level vegetation change that occurs in an ecosystem under stress when individuals can no longer resist and populations can no longer recover.	(Falk et al. 2019)
Retrogressions	Disturbance driven successional changes toward new physiognomic types. In general, retrogressions eventually lead to a grassland climax type. Wells also used, "converted", "fire-succession", "successional changes", "gap-phase successions" and "differentiation" as analogous terminologies.	(Wells 1962)
Species redistributions or Species range shifts	Idiosyncratic, climate-driven species responses resulting "in novel biotic communities and rapid changes in ecosystem functioning, with pervasive and sometimes unexpected consequences that propagate through and impact both biological and human communities."	(Pecl et al. 2017)
Linear, threshold or hysteresis dynamics	These are complex ecosystem interactions, often in the form of positive feedbacks, that can magnify small changes and cause rapid change across thresholds toward an alternative state and/or function. Often, there is increasing variability or rising standard deviations after the perturbations.	(Suding and Hobbs 2009)
Thresholds and breakpoints in ecosystems	"models [united] by the common theme of possessing a regime of dynamical behavior in which there are two alternative stable states, so that continuous variation in a control variable can produce discontinuous effects." Alternative stable states	(May 1977)
Tipping point	This is "Any situation where accelerating change caused by a positive feedback drives the system to a new state." "Our proposed	(van Nes et al. 2016)

	definition essentially boils down to the necessary conditions [where] a small initial change makes a big difference.”	
Transformed landscapes	Climate- and/or disturbance induced forest conversions to non-forest resulting in altered “ecosystem services such as watershed integrity, wildlife habitat, aesthetics, and recreation”	(Parks et al. 2019)
Transitions	“As a result of disturbances that affect species composition, forests convert to new forest types but retain primary ecosystem functions and services. The transition results from changes in species abundances or the loss of one or more minor species. “	(Millar and Stephenson 2015)
Vegetation type- conversion	A process of vegetation change.	(Haidinger and Keeley 1993, Kimball et al. 2014, Syphard et al. 2018)