A succession of theories: purging redundancy from disturbance theory

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ABSTRACT

The topics of succession and post-disturbance ecosystem recovery have a long and convoluted history. There is extensive redundancy within this body of theory, which has resulted in confusion, and the links among theories have not been adequately drawn. This review aims to distil the unique ideas from the array of theory related to ecosystem change in response to disturbance. This will help to reduce redundancy, and improve communication and understanding between researchers. We first outline the broad range of concepts that have developed over the past century to describe community change in response to disturbance. The body of work spans overlapping succession concepts presented by Clements in 1916, Egler in 1954, and Connell and Slatyer in 1977. Other theories describing community change include

state and transition models, biological legacy theory, and the application of functional traits to predict responses to disturbance. Second, we identify areas of overlap of these theories, in addition to highlighting the conceptual and taxonomic limitations of each. In aligning each of these theories with one another, the limited scope and relative inflexibility of some theories becomes apparent, and redundancy becomes explicit.

We identify a set of unique concepts to describe the range of mechanisms driving ecosystem responses to disturbance. We present a schematic model of our proposed synthesis which brings together the range of unique mechanisms that were identified in our review. The model describes five main mechanisms of transition away from a post-disturbance community: (1) pulse events with rapid state shifts; (2) stochastic community drift; (3) facilitation; (4) competition; and (5) the influence of the initial composition of a post-disturbance community. In addition, stabilising processes such as biological legacies, inhibition or continuing disturbance may prevent a transition between community types. Integrating these six mechanisms with the functional trait approach is likely to improve the predictive capacity of disturbance theory.

Finally, we complement our discussion of theory with a case study which emphasises that many post-disturbance theories apply simultaneously to the same ecosystem. Using the well-studied mountain ash (*Eucalyptus regnans*) forests of south-eastern Australia, we illustrate phenomena that align with six of the theories described in our model of rationalised disturbance theory. We encourage further work to improve our schematic model, increase coverage of disturbance-related theory, and to show how the model may link to, or integrate with, other domains of ecological theory.

Key words: life-history traits, resource gradient, vital attributes, facilitation, tolerance, inhibition, initial floristic composition, habitat accommodation, neutral metacommunity, intermediate disturbance hypothesis.

CONTENTS

I. INTRODUCTION

It is important for ecologists and land managers to understand the influence of disturbance on ecosystems. This is because the encroachment of humans on natural ecosystems and climate change are altering disturbance regimes and placing increasing pressure on ecosystem services and biodiversity (Brennan, Christie & York, 2009;Eigenbrod *et al.*, 2011). Land managers need to understand how ecosystems react to disturbances so that they can manage natural resources in an informed and effective way (Chesson, 1991;Hunter, 2007;Turnbull, Crawley & Rees, 2000). Disturbances such as fire, windstorms and floods can have major positive and negative impacts on both natural and human-modified ecosystems. In natural ecosystems, disturbances can alter the abundance and diversity of species, and influence nutrient and energy cycling, biomass accumulation, primary production, hydrological regimes and other key ecosystem processes (Sousa, 1984;Swanson *et al.*, 2011). Some negative impacts of disturbance include direct mortality of animals and plants (Keith, McCaw & Whelan, 2002), as well as the destruction of resources and habitats (White & Pickett, 1985). However, disturbances often produce highly variable landscapes, which are essential for many species (Sousa, 1984). They also may increase biodiversity by creating new habitats and making new resources available (Connell, 1978;Lindenmayer, 2009a).

Numerous theories explore how ecosystems respond to disturbances, ranging from the classic Clementsian view of succession (Clements, 1916) to the more recently popularised biological legacy concept (Franklin *et al.*, 2000). In this broad field of disturbance, many theories and ideas have been developed that are similar, have overlapping concepts, or have conflicting definitions. For example, the core mechanisms of Connell & Slatyer's (1977) tolerance model were previously well described as the fugitive species concept (Elton, 1927;Horn & Mac Arthur,

1972;Hutchinson, 1951). In both of these theories, good dispersers colonise first, growth of these early colonists makes the habitat less suitable for additional early colonist species, slowly dispersing, strong competitors can invade and outcompete the early colonists, and in the absence of further disturbance, the good dispersers are eliminated. The term "fugitive species" itself also has a range of synonyms including "opportunists" (MacArthur, 1960), "pioneering species" (Wynne-Edwards, 1962) and "ephemeral species" (Gilbert *et al.*, 1976). Other examples of this redundancy of terms include: much overlap in invasive species hypotheses (see Catford, Jansson & Nilsson, 2009), the plethora of redundant terms that are used for ecological stability concepts (Grimm & Wissel, 1997) and many definitions for terms such as niche (McInerny & Etienne, 2012).

This kind of redundancy poses potential problems for scientists and land managers; it can make communication difficult and it fosters isolated areas of research where the same discoveries are repeated and communicated using different sets of words (Driscoll & Lindenmayer, 2012). For example, Connell & Slatyer (1977) suggested there was little support for the tolerance model of succession, when in fact substantial evidence existed in the fugitive species literature (e.g. Horn & Mac Arthur, 1972;Hurley, 1973;Hutchinson, 1951). Ultimately, such conceptual redundancy can impede scientific progress because research effort is divided into different silos (Austin, 1999;Driscoll & Lindenmayer, 2012). There may be circumstances where interaction among conceptual silos leads to scientific advancement, such as when broader fields of biology interact (Cagnacci *et al.*, 2010;Stockwell, Hendry & Kinnison, 2003). Nevertheless, it remains possible that such advances would happen faster if the silos had not been formed in the first place.

We review theory on succession and disturbance, to identify overlap among, and differences between, these theories. A framework emerges from this review that provides a simplified set of

theories that can assist in improving and directing research, as well as facilitating communication about these topics. Our review has four main parts. Section II describes the broad range of theories that has been developed on succession and disturbance. Section III brings together these theories and discusses the overlap and differences between these ideas to pin down redundancy and identify unique phenomena. In Section IV we synthesise these unique phenomena into a simple conceptual framework that represents rationalised theory as advocated by Driscoll & Lindenmayer (2012). Rationalised theory arises from a synthetic review of the theory describing a set of phenomena, within a defined domain (Driscoll & Lindenmayer, 2012). Section V is a case study that provides a demonstrative example of many of the core ideas identified in the rationalised framework of disturbance-related theory.

In this review, we use the term 'theory' in a broad sense, where a theory consists of a testable hypothesis, and the associated assumptions and concepts. We use the term disturbance to refer to "any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability, or the physical environment" (White & Pickett, 1985, p. 7).

II. SUCCESSION AND DISTURBANCE THEORIES

For many years, ecologists have attempted to predict how ecosystems will change after disturbance. Many hypotheses have been proposed to predict or explain successional pathways and explain patterns of biological diversity. However, no one theory has been universally agreed upon. This is, in part, due to the complexity and variability of the ecosystems and disturbance events involved (Kayes, Anderson & Puettmann, 2010). Influential theories about vegetation succession include Clements' (1916) early ideas on facilitation and climax states, the Initial

Floristic Composition model by Egler (1954) and Connell & Slatyer's (1977) three hypotheses of Facilitation, Tolerance and Inhibition. These early theories need to be examined to build a thorough synthesis of disturbance-related concepts. More recently, successional theories have been applied to animals, building on the work done on plant succession, with the Habitat Accommodation Model being a prominent example (Fox, 1982). In this section, we discuss some of the more influential theories of succession and diversity.

The literature related to disturbance is large. Therefore not all theories can be covered in this review, although we have examined the most important ones. For example, theories explaining patterns of species diversity such as niche models (Grinnell, 1924;Peterson, 2006;Soberón & Peterson, 2005), lottery models (Chesson, 1991;Sale, 1977;Turnbull *et al.*, 2000), pattern diversity (Pielou, 1966) and patch dynamics (White & Pickett, 1985;Wu & Loucks, 1995) are less directly relevant to the topic of succession and post-disturbance ecosystems than the succession and other disturbance-related theories that we have addressed.

In this review, we largely focus on post-disturbance succession. Succession is sometimes split into primary succession and secondary succession. Primary succession occurs in areas that are lacking previous life or soil structure such as newly emerged land, e.g. dunes or lava flows (Campbell, Reece & Meyers, 2006;Clements, 1916;Cutler, 2011). Extreme disturbance can initiate this kind of succession (Walker & del Moral, 2003). Disturbance often initiates secondary succession in which the soil is somewhat intact and frequently contains high numbers of germules from before disturbance (Campbell *et al.*, 2006;Clements, 1916).

Succession also can be classified as progressive or retrogressive. Progressive succession is a period of biomass increase while retrogressive succession is a possible subsequent period of biomass and soil loss, which can occur in a system that has not experienced a major disturbance

in a long time (Walker & Reddell, 2007). The concepts described herein apply equally well to both kinds of succession, because both describe ongoing community change in the absence of disturbance.

(1) Early plant succession theories

Literature on succession began perhaps with King (1685) and gained momentum in the 1800s (Hult, 1885 (article not seen in English, cited in Clements, 1916);Thoreau, 1860). In the early 1900s researchers such as Clements (1916) and Cowles (1901;1911) published ideas that have continued to influence thinking on succession. Each of the early concepts of succession discussed below has played a large part over the last century in shaping the discussion on succession. We will later show how this early work reappears in different guises in more recent disturbance-related theory.

(*a*) *Clements*

Clements' (1916) theories strongly shaped thinking on succession in the 20th century. He framed succession as occurring in a directional and predictable manner, commencing from a "bare state" and progressing from pioneer species to a "climax" or final stage. Clements (1916) saw succession as a series of invasions, starting with pioneer species, with each stage in turn being invaded by a "higher" form (Clements, 1916). Established species alter environmental conditions so that they are less favourable for themselves and potentially more favourable to species from the next stage. This occurs until conditions are most favourable to the current set of species and the climax stage is achieved (Clements, 1916, pp. 74, 80).

The idea of a climax or final equilibrium state was central to Clements' (1916) ideas, but today ecologists generally disagree with this idea and view systems as dynamic, complex and non-equilibrial in nature (Connell, 1978;Connell & Slatyer, 1977;McIntosh, 1999;Moore *et al.*, 2009;Sousa, 1984). Other problems with Clements' (1916) ideas include his overly deterministic view that succession is entirely predictable and orderly and his heavy use of jargon, which makes his ideas inaccessible to modern readers (McIntosh, 1999).

(*b*) *Cowles and Gleason*

Cowles' (1901,1911) work preceded much of Clements (1916) writing on succession. His most influential comment on the subject was that succession is "a variable approaching a variable rather than a constant" (Cowles, 1901). This is a very different idea to Clements' (1916) directional and deterministic views and suggests that succession is not a linear process with a defined end point, but rather a complex dynamic process that can even go "backwards" and is without a certain end point. Cowles' (1901) comment still resonates with some modern ecologists more so than Clements' deterministic ideas (eg. McIntosh, 1999;Prach & Walker, 2011;Sheil, 1999).

Gleason (1917,1927) was one of the early opponents of many of Clements' (1916) ideas, advocating that succession phenomena were due to individual plants' characteristics. However, Gleason's (1917,1927) ideas were comparatively ignored. He disagreed with the idea of a climax state and instead believed that succession was "constant and universal" (Gleason, 1927), an idea that continues to influence modern thinking (McIntosh, 1999;Pickett, Cadenasso & Meiners, 2009). By this comment, he meant that succession is a continuous process that has no end point.

He also thought that the first organisms to leave the system were those least tolerant to changing environmental conditions.

(*c*) *Egler – Relay Floristics and Initial Floristic Composition*

Conceptually, Relay Floristics is essentially deterministic changes from pioneer to climax species, but applied to abandoned agricultural land, or "old-fields". In Relay Floristics, groups of species successively appear and disappear from a site (Fig. 1A). A group will enter the site at a specific stage and then make the conditions unsuitable for themselves and more suited for the next group to invade. This will continue until a stable climax stage is reached (Egler, 1954). Based on his work on "old-fields", Egler (1954) also proposed the Initial Floristic Composition model, as an alternative to Clementsian succession. In his model, an area obtains various propagules until abandonment by human management, after which no further invasion by additional species takes place. All plant species and stages begin to develop from the start, with herbaceous species initially dominant because they are fast-growing. Each stage – herbaceous weeds, grassland, shrubland and finally forest – becomes predominant and then drops out in turn, until only trees dominate in an "equilibrium" state (Fig. 1B). The different stages drop out due to differential longevity, with each successive stage having a longer lifespan. Egler (1954) also alluded to the ability of a species to resist invasion, which is independent of the plant's position in the succession, as being an important stabilising factor and varying according to species and abiotic factors.

Further invasion may occur during this process through Relay Floristics and alter the successional pathway. Egler (1954) saw both Relay and Initial Floristics as ideal cases, and that

in reality, both would work in conjunction with each other and with other factors such as herbivory, disturbance, disease, pests and invasion of rhizomes.
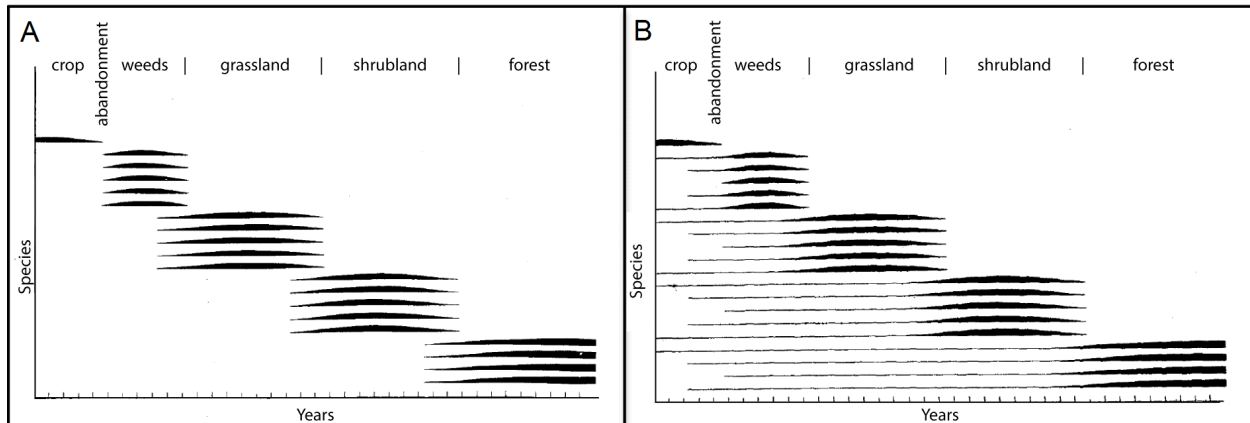
Fig. 1. Two contrasting vegetation successional pathways. (A) Relay floristics. Groups of species successively enter and leave the site. Species make the conditions unsuitable for themselves and more suitable for later species. (B) Initial floristics composition. All species are present from the beginning and each group drops out in turn until only trees dominate in an equilibrium state. Modified from Egler (1954, pp. 414 – 415).

Researchers continue to test Egler's models with mixed results. For example, Kayes *et al.* (2010) examined post-fire recovery of Douglas fir (*Pseudotsuga menziesii*) forests and found that succession followed the Initial Floristic Composition model. However, the majority of studies across a range of vegetation types and geographical areas have found mixed results between scales, stages and vegetation types with some aspects of their studies matching one or both of Egler's models but others not (e.g. Copenheaver, 2008;McClain, Holl & Wood, 2011;Penman *et al.*, 2011).

(*d*) *Fugitive species*

Hutchinson (1951) formalised the concept of fugitive species, noting that the degree of originality of this concept was "inconsiderable" (Elton, 1927). Species that are good dispersers

but poor competitors may survive in a landscape that is subject to disturbance by arriving, establishing and breeding in sites before good competitors arrive (Horn & Mac Arthur, 1972;Questad & Foster, 2007). Increasing abundance of fugitive species makes it increasingly difficult for additional fugitive species to colonise (Horn & Mac Arthur, 1972). However, when slower-dispersing but strongly competing species arrive, the poor competitors are eliminated (Hutchinson, 1951).

(*e*) *Early animal succession*

While early studies of succession were dominated by work on plants, a number of ecologists studied animal succession. Shelford (1907;1911) examined succession in tiger beetles and pond fishes. Shelford (1907;1911) hypothesised that plant succession was a driver of animal succession, with changing vegetation bringing in, and driving out, different animal species. Other early work such as that by Adams (1908) examined succession in North American birds. Contrasting with Shelford (1907), Adams (1908), argued that both internal (biotic) and external (physical or environmental) factors were drivers of faunal succession. From the 1960s, studies of animal succession began to increase, particularly those examining aquatic environments (e.g. Dean & Connell, 1987;Fish & Hall, 1978;Smith, 1968).

(2) Facilitation, Tolerance and Inhibition
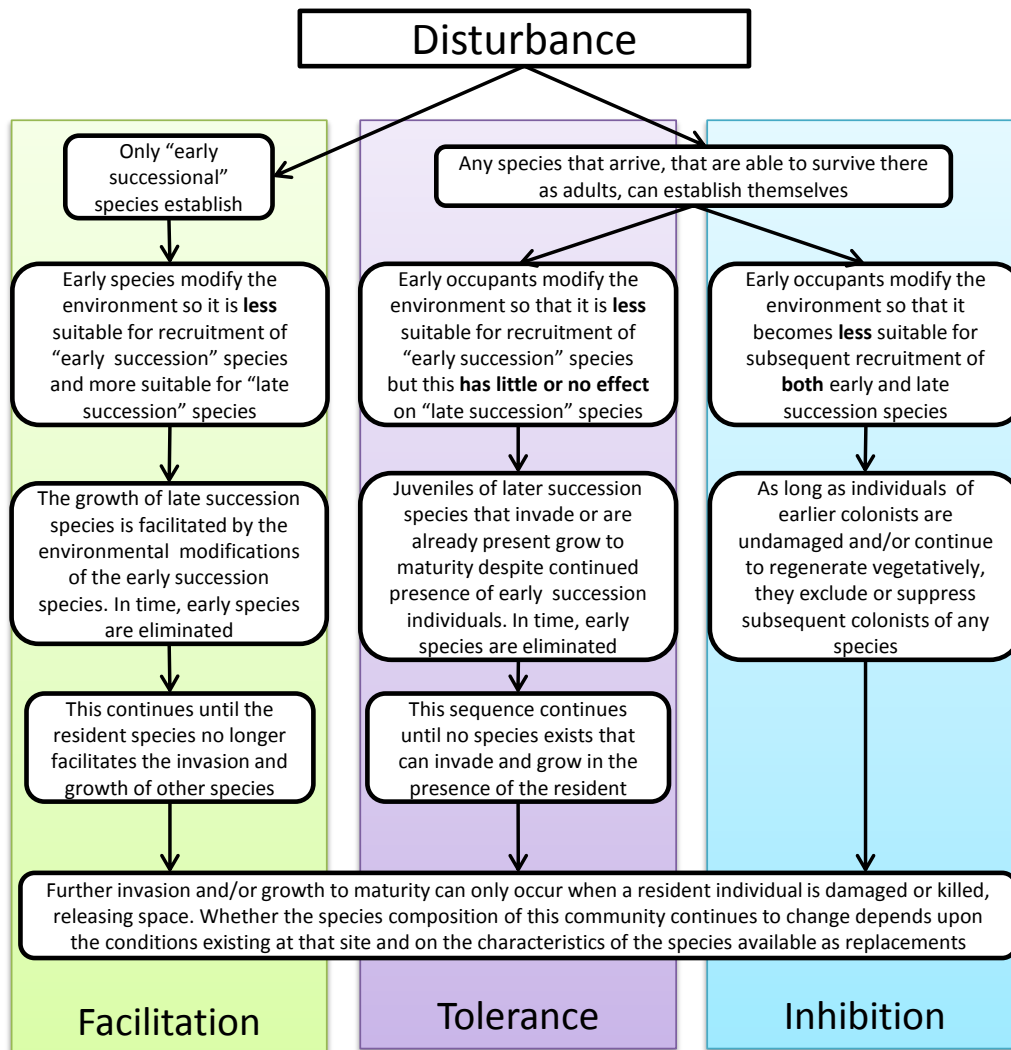
(*a*) *Connell and Slatyer*

Connell & Slatyer (1977) developed three succession models: Facilitation, Tolerance and Inhibition. The Tolerance and Inhibition models assume that any species that arrives at a site has

the potential to colonise. In contrast, the Facilitation model assumes that only early successional species or "pioneers" are initially able to colonise. Connell & Slatyer (1977, p. 1132) viewed the three models as representing "the process by which a community recovers from a perturbation".

In the Facilitation model (Connell & Slatyer, 1977) early pioneer species alter conditions so that they are less suitable to themselves and more suitable to later successional species, which then colonise. Put another way, early species facilitate the entry of later species (Fig. 2). Connell & Slatyer (1977) concluded that the Facilitation model was most likely to occur in some cases of primary succession and animal succession.

In the Tolerance model (Connell & Slatyer, 1977), later species successfully establish themselves if they are more tolerant to low levels of resources and therefore outcompete preceding species. They do not need early-stage species to alter the conditions for them. Early colonisers make conditions less suitable for "early succession" species but do not affect "late succession" species (Fig. 2).

In the Inhibition model (Connell & Slatyer, 1977), early colonising species inhibit the establishment and development of other individuals until they die or are damaged. Established species alter conditions so that they are less suitable for both early and late succession species (Fig. 2). Because short-lived species will have higher turnover than long-lived species, there are more opportunities for short-lived species to be replaced than for longer-lived species (Connell & Slatyer, 1977). As a consequence, inhibition theory predicts gradual sequential succession from short- to long-lived species. Connell & Slatyer (1977) concluded that for vegetation succession, the literature at that time showed more support for this model than for the Tolerance and Facilitation models.

Fig. 2. The processes of Connell & Slatyer's (1977) three succession models: facilitation, tolerance and inhibition. Modified from Connell & Slatyer (1977).

Numerous studies have found evidence that a range of mostly sessile organisms appear to support (or partially support) one or more of Connell & Slatyer's (1977) models in ecosystems such as benthic communities, forest stands, and coral reefs (e.g. Bergeron, 2000;Copenheaver, 2008;Dean & Hurd, 1980;Mullineaux *et al.*, 2003). Many studies also acknowledge that one or more of these models may be acting at once and that they are not mutually exclusive (e.g. Connell & Slatyer, 1977;Dean & Hurd, 1980;Rogers, 1993). For example, Kim (1997) found that

early colonising species of algae inhibited the colonisation of two other species but that this occurred only in the absence of limpets. When limpets were present, the colonising ephemeral algae were heavily grazed and therefore unable to fully inhibit the later successional algae.

(*b*) *Habitat Accommodation model*

Connell & Slatyer's (1977) Facilitation and Tolerance models were adapted by Fox (1982) into the Habitat Facilitation, and Habitat Tolerance models, respectively (Fox, 1982;Fox, Taylor & Thompson, 2003) and resulted in the Habitat Accommodation model. The model states that post-disturbance recovery of animal species is related to the vegetation assemblage (Fox, 1982). In the Habitat Accommodation model, an animal species will establish in an ecosystem when the vegetation structure and composition first meets their habitat requirements (the habitat facilitation part of the model). Species will then decline or be excluded when the vegetation structure and composition changes, and is therefore no longer suitable for them and/or better-suited species outcompete them (the habitat tolerance part of the model) (Fox, 1982;Fox *et al.*, 2003) (see Fig. 3). In the Habitat Accommodation model, animals react to their physical environment but do not alter it (Fox, 1982).
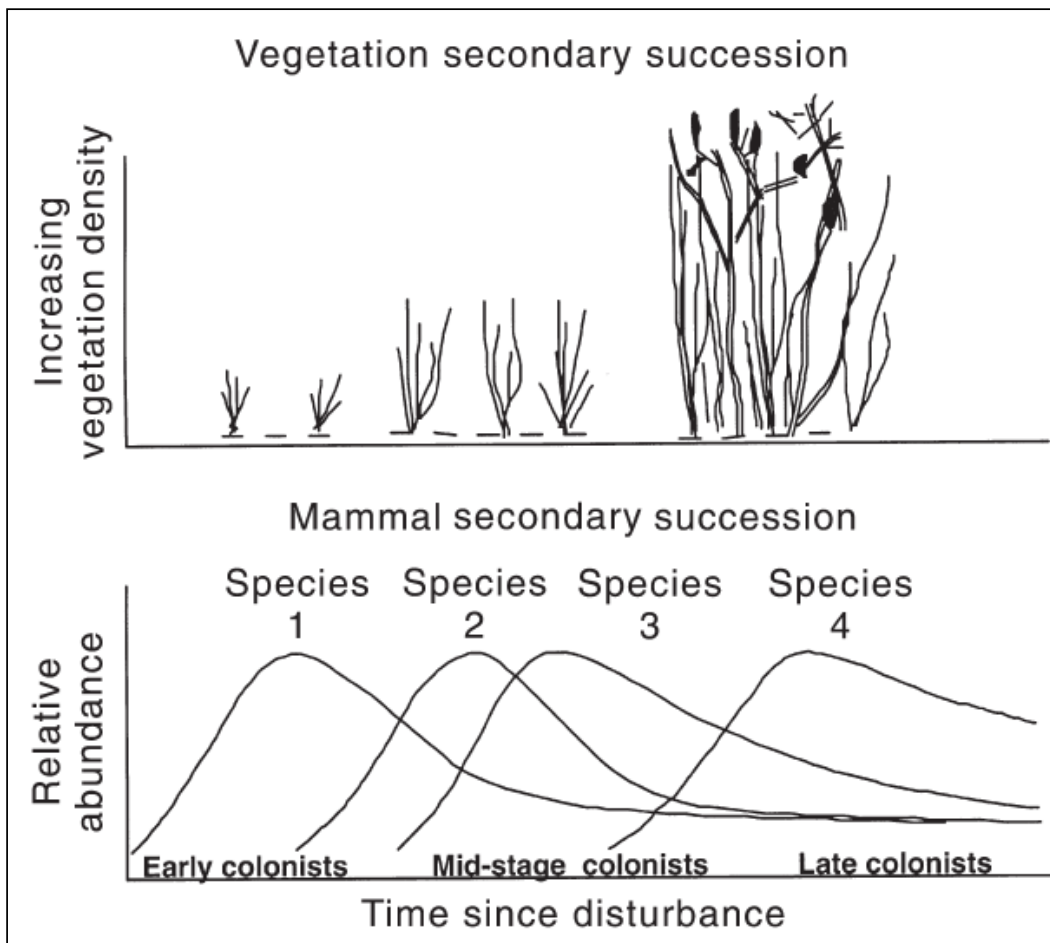
Fig. 3. The habitat accommodation model: a diagrammatical representation. Animal species enter when the vegetation reaches their requirements and exit when the vegetation moves out of their requirement range. Source: Monamy & Fox (2000, p. 581).

There have been mixed results from studies testing the Habitat Accommodation model. In wet heath in eastern Australia, Fox *et al.* (2003) discovered an association between changes in habitat structure and the turnover of rodent species, as predicted by the Habitat Accommodation model. However, other studies have found that the Habitat Accommodation model is a poor predictor of the responses of some other taxa [e.g. reptile responses to fire in Australia (Lindenmayer *et al.*, 2008b;Nimmo *et al.*, 2012;Smith, Bull & Driscoll, 2013)]. The Habitat Accommodation model was formulated from studies of small mammals and may be most applicable to this group.

(*c*) *Intermediate Disturbance Hypothesis*

The Intermediate Disturbance Hypothesis predicts change in species richness in relation to rates of disturbance so that communities with intermediate levels of disturbance will support the greatest number of species (Connell, 1978;Grime, 1973). Variation in disturbance could occur in frequency, extent, intensity, duration or time since disturbance (Shea, Roxburgh & Rauschert, 2004). At low levels of disturbance, the most competitive species come to dominate. At high levels of disturbance, only extremely resistant species or rapid colonisers will manage to reach maturity between disturbance events (Connell, 1978;Wilson, 2011). At intermediate levels of disturbance, more species may co-exist due to lower competition, varying rates of response to resource availability or a competition–colonisation trade-off (Fox, 2013;Shea *et al.*, 2004). Of studies that examine this hypothesis, less than 20% have found support (Mackey & Currie, 2001), and Fox (2013) suggested the hypothesis should be abandoned because of its narrow scope.

(3) Resource and trait-based hypotheses

Several authors have suggested that the gradients of resources or stresses in an ecosystem influence succession, and that these gradients interact with species' traits to determine community change (e.g. Drury & Nisbet, 1973;Grime, 1979;MacArthur & Wilson, 1967;Tilman, 1985). These theories have slightly different foci or levels of complexity and a number of these theories are discussed below. All of these concepts relate to the categorisation of life-history traits, and more focused life-history trait approaches are discussed at the end of this sub-section (e.g. Noble & Slatyer, 1980;Whelan *et al.*, 2002).

(*a*) *Differential growth and differential survival – Drury and Nisbet*

Drury & Nisbet (1973) adapted Odum's (1969) tabular model of succession that combines temporal succession of vegetation with spatial changes along environmental gradients. They considered that, in general, the succession of species was determined by "differential growth, differential survival (and perhaps differential colonising ability)" along environmental gradients (Drury & Nisbet, 1973, p. 362). For example, Monk (1983) studied old-field succession in the Georgia Piedmont, USA and found that the three factors suggested by Drury & Nisbet (1973) were important drivers of succession in that ecosystem.

More recently, Pickett & McDonnell (1989) and Pickett *et al.* (2009) proposed that a similar general set of parameters to that suggested by Drury & Nisbet (1973) drive vegetation succession (vegetation dynamics). These parameters are differential site availability, differential species availability, and differential species performance.

(*b*) r- *and* K-*selection*

The concept of *r*- and *K*-selection suggests that there are two ends of the selection spectrum (*r* and *K*) that affects an organism's ability to colonise and persist in an environment (MacArthur & Wilson, 1967). *K* is the "carrying capacity of the environment" and *r* is the "per capita rate of increase in a given unit of time" (MacArthur & Wilson, 1967). Commonly attributed characteristics of *r*-selected individuals include early maturity, short life cycle and many offspring. *K*-selected individuals typically take a long time to mature, have a long life cycle and produce few offspring. After a disturbance, colonising species are expected to have characteristics of *r*-selection and the traits of colonising species progress to *K*-selection as the

available resource levels stabilise and competition increases. The prominence of either *r*- or *K*-selection will then be determined by the stability of resource levels in the environment (MacArthur & Wilson, 1967).

The concept of *r*- and *K*-selection has been interpreted in a number of ways (see Parry, 1981), which makes the concept hard to assess empirically. Numerous authors have attempted to use this concept to examine life-history traits of organisms, but there has been a general move away from this concept due to many examples where the theory is not robust (Lankau & Strauss, 2011). Alternative methods of categorising life-history traits are discussed below.

(*c*) *CSR theory*

Grime's (1979;2001) theory of C-, S-, and R-selection suggests that there are three selection pressures on plants that result in three strategies or functional types: competitive (C), stress tolerant (S) and ruderal (R) (Fig. 4). After disturbance, succession proceeds from the bottom right hand corner of the diagram (maximum influence of disturbance) towards the C–S side of the triangle (Fig. 4). The pathway towards the C–S axis will be determined by the level of stress (e.g. productivity of the soil, shading etc.), which can change throughout the succession (Grime, 1979). Despite the CSR theory generating a lot of discussion, it has only rarely been empirically tested in terrestrial ecosystems, most likely due to the difficulty in defining and testing some aspects and assumptions (e.g. it is challenging to define the intensity of competition) (Wilson & Lee, 2000). The CSR theory has been more thoroughly investigated in aquatic ecology, where it is often found to be too simplistic (e.g. Reynolds, 1998) and does not describe the suite of traits found in aquatic plants (e.g. Willby, Abernethy & Demars, 2000).
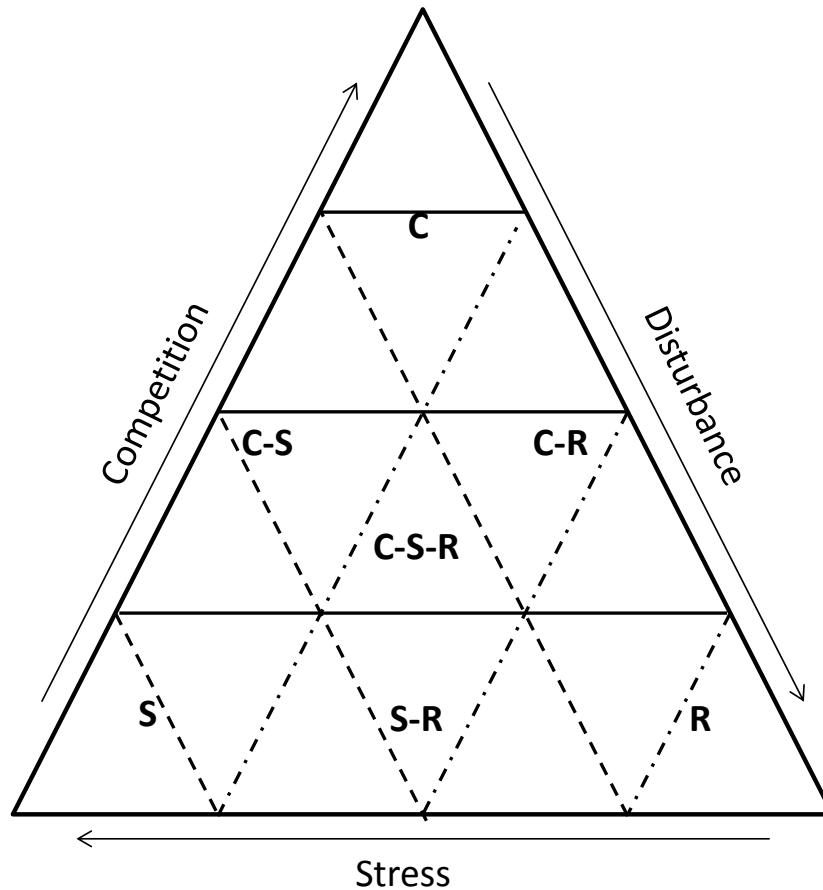
Fig. 4. Simplified version of the CSR triangle. Arrows indicate increasing importance for each factor (competition, stress and disturbance) and letters represent competitive (C), stress tolerant (S) and ruderal (R). Modified from Grime (1979).

Wonkka *et al*. (2012) used the CSR theory to classify North American trees into life-history categories and analysed ice storm damage data to examine how this form of natural disturbance affected the different categories. They found that the CSR categories corresponded with the damage sustained. For example, the stress tolerant (S) species were the least damaged by the disturbance (Wonkka *et al.*, 2012).

Other models similar to the CSR concept have been proposed. One such model is the Logistic Simulation model (Whittaker & Goodman, 1979), which proposes three broad categories of a population's carrying capacity according to the variation in environmental conditions. These

three patterns are: adversity selection (hostile environments), exploitation selection (variable and sporadically favourable environments), and saturation selection (competition in a favourable environment) (Whittaker & Goodman, 1979). This model is broadly applicable to both plants and animals.

(*d*) *Resource Ratio Hypothesis*

The Resource Ratio Hypothesis (Tilman, 1985) proposes that plant succession is driven by the amounts of limiting resources (soil nutrients, light and sometimes water) that are available and which may be altered by disturbances. Plant species are adapted to different quantities of these limiting plant resources and a change in availability of these resources will result in a change in community composition (Tilman, 1985). Prior to 1985, Tilman and other authors suggested broader resource ratio theories (e.g. MacArthur, 1972;Tilman, 1980;Tilman, 1982).

(*e*) *Life-history trait-based approaches*

In the past 30 years, a new approach to using life-history traits for predicting responses to disturbance has flourished. Rather than coarse classifications of taxa into a few simple groups that is encouraged by *r*- and *K*-selection and CSR concepts, approaches based on grouping species according to shared life-history traits have produced finer-scaled classifications and in some cases achieved substantial predictive success (Keith *et al.*, 2007;Noble & Slatyer, 1980). One of the early and most influential examples of a trait-based approach was the "vital attributes" approach developed by Noble & Slatyer (1980). This approach uses the life-history traits or "vital attributes" of potentially dominant species to model vegetation dynamics after disturbance. This model has been used repeatedly to examine post-disturbance responses of

vegetation communities with much success (e.g. Bradstock & Kenny, 2003;Keith *et al.*, 2007;Pausas, 1999). For example, Keith *et al.* (2007) used the plant functional types approach, which is based on vital attributes, to model vegetation dynamics in fire-prone wet heathland of south-eastern Australia. The approach provided good predictions of the average vegetation change over the 21-year period examined (Keith *et al.*, 2007).

Plant functional types are groups of plants that respond in a similar manner to conditions and disturbances, and affect ecosystem processes in a similar way (Díaz Barradas *et al.*, 1999;Gitay & Noble, 1997;Root, 1967). There has been a lot of research effort into developing plant functional types that assist with land management and monitoring environmental change (Lavorel *et al.*, 2007). Despite a large amount of work directed towards developing a single comprehensive classification system of plant functional types, this goal remains elusive (Lavorel *et al.*, 2007;McIntyre *et al.*, 1999). The disconnect between traits that determine ecosystem function and the traits that determine responses to environmental factors is a major challenge for this area of research (Lavorel *et al.*, 2007). Another challenge is the vast array of definitions for the term "plant functional types" (Gitay & Noble, 1997).

Another trait-based approach is the "critical life cycles" approach, which is applicable to both animals and plants (Whelan *et al.*, 2002). The critical life cycles approach suggests that understanding the processes that result in patterns of response (e.g. to fire) should be combined with knowledge of the life cycle of an organism, as well as knowledge of local environmental factors such as climate, fire history and landscape characteristics. The possible processes that may affect animal fire responses that were suggested by Whelan *et al.* (2002) include direct mortality resulting from the fire, recolonisation, survival and establishment of individuals after fire, and post-fire reproduction and population growth.

Trait-based approaches have generally been used with less success for animals than for plants. For example, Langlands *et al.* (2011) adapted the concepts of "vital attributes" and "critical life cycles" (Noble & Slatyer, 1980;Whelan *et al.*, 2002), as well as using functional understanding of spider traits to develop predictions of spider responses to fire in Western Australia. While they found significant associations between time since fire and a number of traits (e.g. body size), many of the traits explored did not conform to predictions and many others were important only briefly after a fire. There is much research that attempts to link traits with wildlife response to disturbances such as grazing (Hanspach *et al.*, 2012;Silver & Vamosi, 2012), habitat loss (Davies, Margules & Lawrence, 2000;Driscoll & Weir, 2005) and fire (Lindenmayer *et al.*, 2008b;Moretti *et al.*, 2009;Moretti & Legg, 2009;Smith *et al.*, 2013). Nevertheless, universally applicable and general patterns linking traits to disturbance response have not yet emerged, and the predictive value generally remains low. While some studies have made progress in this direction (e.g. Latzel *et al.*, 2011), perhaps the way ecologists go about examining this issue needs a shift in approach. One suggestion is to move away from pairwise analysis and instead examine the problem by focussing on four themes: traits, environmental gradients, the interaction milieu (i.e. the background of biotic interactions in which the organism interacts) and performance currencies (e.g. energy intake) (McGill *et al.*, 2006).

(4) Stochastic effects

A rather different approach to the theories discussed so far are stochastic succession models (e.g. Holyoak, Leibold & Holt, 2005;Horn, 1975;Hubbell, 2001;Van Hulst, 1979). Markovian chains are a stochastic statistical process where transitions between a finite number of states are determined by the state immediately previous and not by any factors further into the past (Horn,

1975;Kemeny & Snell, 1960, p. 207). Horn (1975) presents an example of a Markovian stochastic succession model examining cell by cell (tree-by-tree) replacement to calculate the probability that a tree will be replaced by one of its own species or by another species, as determined by the frequency of juveniles of each species. This allows the calculation of the number of trees from each species that should be present at a particular stage in succession (Horn, 1975).

Baasch, Tischew & Bruelheide (2010) used Markovian models to estimate vegetation regeneration for more than 20 years from the beginning of the successional cycle in post-mine sites in Germany. Their proposed methods were relatively successful, with the vegetation composition observed more than two decades after a disturbance generally agreeing with the predictions of the models.

A conceptually similar idea to stochastic succession models is neutral metacommunity theory. This idea suggests that all the trophically similar species and individuals in a number of local communities within a region are competitively equivalent (Hubbell, 2001). Consequently, changes in community composition occur through ecological drift; a result of stochasticity associated with births, deaths, immigration and emigration (Holyoak *et al.*, 2005;Hubbell, 2001).

(5) State and transition models

The ideas of resilience and multiple stable states (Holling, 1973;May, 1977;Scheffer *et al.*, 1993) opened the way for state and transition models as a new way of viewing and managing the effects of disturbance in natural and human-manipulated ecosystems (Westoby, Walker & Noy-Meir, 1989). State and transition models assume there are a number of states in which a system can exist, but there are specific conditions that can drive the system between states (Phillips,

2011;Westoby *et al.*, 1989). The transition rate can vary from gradual [e.g. overgrazing (Stringham, Krueger & Shaver, 2003)] to abrupt [e.g. frequent fire can cause a rapid change of dominant vegetation in a forest (Lindenmayer *et al.*, 2011)]. State and transition models are developed using information from a combination of sources including expert knowledge, historical observations, monitoring, controlled experiments, and chronosequence analyses (Bestelmeyer, Goolsby & Archer, 2011). Transitions are driven by events such as natural disturbances (e.g. fire), human management actions (e.g. logging, heavy grazing) or a combination of both (Westoby *et al.*, 1989). These models were originally developed for rangelands (e.g. Briske, Fuhlendorf & Smeins, 2005;Westoby *et al.*, 1989), but have subsequently been used to investigate a wide variety of ecosystems (Letnic *et al.*, 2004;Phillips, 2011). Phillips (2011) identified three basic types of state and transition models: (1) sequential – linear (A→B→C) or cyclical (A→B→C→A); (2) radiation – one state can transition to or from a number of other states; and (3) maximum connectivity – where any state can transition to any other.

State and transition models can be a good tool for examining natural systems by providing managers with better ways of understanding and communicating changes in the ecosystem (Breshears *et al.*, 2002;Westoby *et al.*, 1989). State and transition models also provide broad predictive capabilities to assess and estimate potential future changes, given certain management and environmental conditions. However, the predictive powers of state and transition models are relatively low and their ability to deal with uncertainty is limited (Bashari, Smith & Bosch, 2008;Phillips, 2011). Additionally, state and transition models assume that there is a threshold relationship between states A and B, but this is not always true (Lindenmayer, Fischer & Cunningham, 2005).

(6) Biological legacies

Very few disturbances result in complete removal of all life (Connell & Slatyer, 1977). The majority of post-disturbance ecosystems retain survivors and other biological legacies (Franklin *et al.*, 2000;Platt & Connell, 2003;Swanson *et al.*, 2011). The ecological and disturbance history of an area can be an important driver in post-disturbance recovery and biological legacies represent this history (Copenheaver, 2008;Drake, 1990;Lindenmayer *et al.*, 2008a).

Biological legacies are organisms, structural legacies and biologically generated spatial patterns that are left after a disturbance (Franklin *et al.*, 2000). Biological legacies are sometimes also called residuals or survivors. Biological legacies include whole organisms, spores, seed banks and fungal hyphae. Structural legacies include dead trees, logs and, in marine environments, dead coral. They can provide other species with habitat, nutrients and shelter (Franklin & MacMahon, 2000). They can "lifeboat" individuals through a disturbance that they would otherwise not survive. For example, invertebrates can survive through fires by sheltering inside logs (Campbell & Tanton, 1981;Ulyshen *et al.*, 2010). Biologically generated spatial patterns include changes in chemical, physical or biological components of the soil such as local acidification or nitrogen-fixing bacteria that influence a localised area of soil (Franklin *et al.*, 2000).

While the concept of biological legacies was occasionally considered in some older successional papers, the idea has received significant consideration only in recent years (e.g. Franklin *et al.*, 2000;Ledger *et al.*, 2006). For example, Griggs (1922) noted the importance of biological legacies or residuals. He reported rapid revegetation of the land almost solely by buried roots,

rather than by new seedlings after the land was buried in a thick blanket of ash from a volcanic eruption in Alaska (Griggs, 1922).

Biological legacies can strongly influence the pathway and rate of ecosystem recovery (Franklin *et al.*, 2000;Platt & Connell, 2003;Swanson *et al.*, 2011). They can influence recruitment of colonists through ecosystem engineering or interspecific interactions, can maintain species diversity and structural complexity, and help to re-establish ecosystem functions (Franklin *et al.*, 2000;Ledger *et al.*, 2006;Swanson *et al.*, 2011). For example, Ledger *et al.* (2006) found that of the three aquatic invertebrates that they studied in post-disturbance streams, a mayfly (*Serratella ignita*) had no discernible effect on subsequent communities, while a snail (*Radix peregra*) greatly influenced the settlement of filter feeders by bulldozing the algal growth, and a freshwater shrimp (*Gammarus pulex*) affected the subsequent communities by reducing or excluding colonists.

III. RELATIONSHIPS BETWEEN THEORIES

Many of the theories and concepts that we have discussed have overlapping or similar ideas, which we synthesise in Table 1 and Fig. 5. Table 1 identifies the overlaps and unique aspects of disturbance-related theory and suggests appropriate and inappropriate applications, helping to define the scope of each theory. It allows researchers to determine when to consider a theory in relation to empirical studies and identifies knowledge gaps for further research. Fig. 5 highlights the relationships and differences between the theories, and provides a quick overview. By highlighting overlap and redundancy, our syntheses in Table 1 and Fig. 5 provide the basis of our rationalisation of disturbance theory (see Section IV).

Table 1. Compilation of a large body of post disturbance and succession theory that examines differences and similarities and suggests appropriate and inappropriate uses for each theory. The cells that have been left blank require further research before they can be filled in.

Concept name	Concept definition	Unique aspects of the concept	Alternative names or overlapping concepts	Appropriate systems and taxa	Inappropriate systems and taxa	Limitations
Facilitation (Clements, 1916; Connell & Slatyer, 1977; Egler, 1954)	Series of invasions from pioneer to late-successional species. Established species make conditions unsuitable for themselves and more suitable for next species in the series	Established species make conditions unsuitable for themselves and more suitable for later colonists	Relay Floristics (Egler, 1954), Clementsian succession (Clements, 1916), Habitat Accommodation model (Fox, 1982)	Primary and secondary succession, animal succession (Connell & Slatyer, 1977)		Assumes predictability and a return to the same sequence after a disturbance. Does not take into account possible abrupt transitions of states. Variable evidence supporting and rejecting
Habitat Accommodation model (Fox, 1982)	Animal succession is determined by vegetation succession. Species moves into and out of the system as vegetation community changes	Vegetation succession drives fauna succession; competitive environment changes over time	Developed from Facilitation and Tolerance models (Connell & Slatyer, 1977. Trait-based approaches	Animals - small mammals in particular (Fox, 1982)	Plants, sessile organisms (Fox, 1982)	Not appropriate for all animal taxa (Lindenmayer et al., 2008b)
Competition (Tolerance) Connell & Slatyer, 1977)	Species that are more tolerant of lower resources will outcompete established species	Emphasises increasing intensity of **competition** with time since disturbance (similar to gradient approaches below)	Large overlap: Gleasonian succession (Gleason 1917, 1927), Intermediate Disturbance Hypothesis (Connell, 1978), Resource Ratio Hypothesis (Tilman, 1985) , Fugitive species (Elton, 1927), Habitat Accommodation model (Fox, 1982)	Variety of organisms and ecosystem types (needs refining)		Assumes predictability and a return to the same sequence after a disturbance. Does not take into account possible abrupt transitions of states. Variable evidence supporting and rejecting

			Gradient hypotheses			
Intermediate disturbance hypothesis (Connell, 1978; Grime, 1973)	Intermediate disturbance results in maximum diversity	Intermediate disturbance results in maximum diversity	CSR theory, Tolerance model (Connell & Slatyer, 1977) (explains low diversity at low disturbance levels)	Tropical systems - e.g. coral reefs and rainforest trees (Connell, 1978; Gunderson, 2000; Knowlton, 1992; Nyström & Folke, 2001)	Does not apply to majority of taxa/ ecosystems (Mackey & Currie, 2001)	Limited to predicting species richness, does not explain composition changes, inadequate focus on mechanisms (Fox, 2013)
Trait-based approaches	Key traits determine species post-disturbance response. Species-level, mechanistic approach	Traits drive succession	Vital attributes (Noble and Slatyer, 1980), Critical life cycle approach (Whelan et al., 2002) etc. Related to Habitat Accommodation Model (Fox, 1982)	Currently works to some extent for plants	Taxa that display little trait differentiation or where little is known about traits	Need to have thorough understanding of traits for the relevant taxa. Made challenging by interactions of traits with other environmental factors Inconsistent definitions (Gitay & Noble, 1997)
Resource Ratio Hypothesis (Tilman, 1985)	Gradients of resources determine succession in combination with species' traits	Amounts of limiting resources (soil nutrients, light and sometimes water)	Other gradient concepts	Dominant species: plants, diatoms, aquatic ecosystems (Miller et al., 2005; Sommer, 1993; Titman, 1976)	Animals (Tilman, 1985)	Does not take into account some factors (e.g. differential colonisation abilities) for simplicity (Tilman, 1985)
Gleasonian succession (Gleason, 1917, 1927), **Drury & Nisbet,** (1973)	Gradients of stress determine succession in combination with species' traits	"Differential growth, differential survival (and perhaps differential colonising ability)" drive succession	Other gradient and trait concepts. Competition model (formally Tolerance) Connell & Slatyer, 1977)	Plants (Drury & Nisbet, 1973; Gleason, 1917, 1927)		

Fugitive species (Elton, 1927; Horn & Mac Arthur, 1972; Hutchinson, 1951)	Species with low tolerance to competition but good dispersal ability are the first to establish in recently disturbed sites and will be outcompeted by more tolerant, poorly dispersing species when the latter arrive	Dispersal ability important factor in success of initial recruits	Other gradient and trait concepts. Competition model (formally Tolerance) (Connell & Slatyer, 1977)			
CSR theory (Grime, 1979, 2001)	Gradients of resources and stress determine succession in combination with species' traits	Three selection pressures applied to plants = three strategies or functional types: competitive (C), stress-tolerant (S) and ruderal (R)	Other gradient and trait approaches, Intermediate Disturbance Hypothesis, r- and K-selection (MacArthur & Wilson, 1967), logistic simulation model (Whittaker & Goodman, 1979)	Plants		Difficult to test some aspects and assumptions (Wilson & Lee, 2000)
r-**and** *K* **selection** (MacArthur & Wilson, 1967)	Gradients of resources determine succession in combination with species' traits	Two ends of selection spectrum (r and K) influence organisms' reproductive strategy	Other gradient concepts, CSR theory (Grime, 1979, 2001), Trait approaches	Has been used successfully for wide range: insects, mammals, and marine invertebrates including a recent study on bacteria (Freilich et al., 2010)	Depends on the definition used (see Parry, 1981)	Many different interpretations of this concept (Parry, 1981)
Inhibition (Connell & Slatyer, 1977)	Early species inhibit further colonisation until they die or are damaged	Established species prevent other species from colonising	Initial Floristics Composition (Egler, 1954)	Sessile organisms, intertidal zones (Connell & Slatyer, 1977; Sousa, 1984)		Does not take into account possible abrupt transitions of states

Initial Floristics Composition (Egler, 1954)	All species are present from the start. Fast-growing species dominate first, and then drop out and slower growing species become dominant	Different species are more dominant at different times in succession according to differential longevity	Old-field succession, Biological legacy (Franklin et al., 2000)	Plant succession in agricultural fields or ecosystems where biological legacies are the main source of species establishment after disturbance		Does not act in isolation (acknowledges that other factors would be affecting succession)
Biological Legacies (Franklin et al., 2000)	Organisms, structural legacies and biologically generated spatial patterns impact the recovery of an ecosystem after a disturbance	Importance of biotic and abiotic biological legacies in post-disturbance response	Residuals (Griggs, 1922), Initial Floristics Composition (Egler, 1954).	Secondary succession (Franklin et al., 2000)	Primary succession (Franklin et al., 2000)	Not very predictive. Does not act in isolation (acknowledges that other factors would be affecting succession)
State and transition (Westoby et al., 1989)	Ecosystems can exist in multiple states. Disturbances can cause transitions between these states. State transitions may be linear in a similar way to succession, radiating or multidirectional between multiple possible states.	Resilience concepts. Ecosystem response to disturbance can be substantial and abrupt rather than continuous	Trait-based approaches also predict multidirectional change in community composition	Range-lands, coral reefs (Briske et al., 2005)	Ecosystem level inference only - not suitable for single taxa	Predictive capacity low (Phillips, 2011). Assumes rapid transition between states, but gradual transitions or continua may exist, as emphasised in succession theories

Stochastic (Horn, 1975; Lawton, 1987; Van Hulst, 1979)	Stochastic models are often Markovian so that transitions between a finite number of states are determined by the current state's characteristics and not by any factors further into the past.	Only the current conditions influence the next state (Markovian models). Community composition drifts due to stochastic demographic and dispersal events	Some similarities to state and transitions models	Markovian models have been applied to tree species (Culver, 1981; Horn, 1975) Neutral models can be used to examine many systems to look at changes in abundance and species richness (Rosindell et al., 2012)	Markovian models are time-consuming to develop. Traditional data-collecting methods (e.g. relevé method) not easily convertible into suitable format for models (Baasch et al., 2010) Neutral models make simplifying assumptions, however these models allow a different method of examining a system (Rosindell et al., 2012)

Idea **Theory** **Description and Differences**

Only pioneer/early successional species can colonise	**Facilitation** →	**Clementsian** (Clements, 1916)
		Relay Floristics (Egler, 1954)
		Facilitation (Connell & Slatyer, 1977)

Series of invasions from pioneer to late successional species. Established species make conditions unsuitable for themselves and more suitable for next in the series

Habitat Accommodation model (Fox, 1982) → Animal succession is dependent on vegetation succession. resources provided by vegetation alter competitive environment

Tolerance (Connell & Slatyer, 1977) → Species that are more tolerant of lower resources will outcompete established species

Gleasonian (Gleason, 1917, 1927) → First to leave the system are the least tolerant

Intermediate Disturbance Hypothesis (Connell , 1978; Grime 1973) → Intermediate disturbance delays competitive exclusion or allows coexistence

Vital attributes, critical life cycles etc. → Key traits determine species post- disturbance response

Drury & Nisbet (1973) → Differential growth, differential survival (and differential colonising ability)

r and *K* selection (MacArthur & Wilson, 1967) → Two ends of the selection spectrum (*r* and *K*) that affects an organism's ability to colonise and persist in an environment

CSR theory (Grime, 1979: 2001) → Three strategies: competitive (C), stress tolerant (S) & ruderal (R)

Resource Ratio Hypothesis (Tilman ,1985) → Different species tolerant to different levels of resources (light and soil nutrients)

Inhibition (Connell & Slatyer, 1977) → Early species inhibit the establishment and development of other individuals until they die or are damaged

Initial Floristics Composition (Egler, 1954) → All species present from start. Groups dominate then drop out in turn

Biological Legacies (Franklin *et al.*, 2000) → Organisms, structural legacies and biologically generated spatial patterns impact the recovery of a site after a disturbance

Residuals → Just considers survivors

State and transition models (Westoby *et al.*, 1989) → Explores the potential states of a system and the possible transitions that may cause a change in state

Markovian succession models (e.g Horn, 1975) → Stochastic process where transitions between a finite number of states are determined by the current states characteristics

Key concept ovals: Facilitation, Tolerance, Trait-based, Gradients, Inhibition, Initial Floristics Composition, Biological Legacies, State & transition models, Stochastic. Any species can colonise.
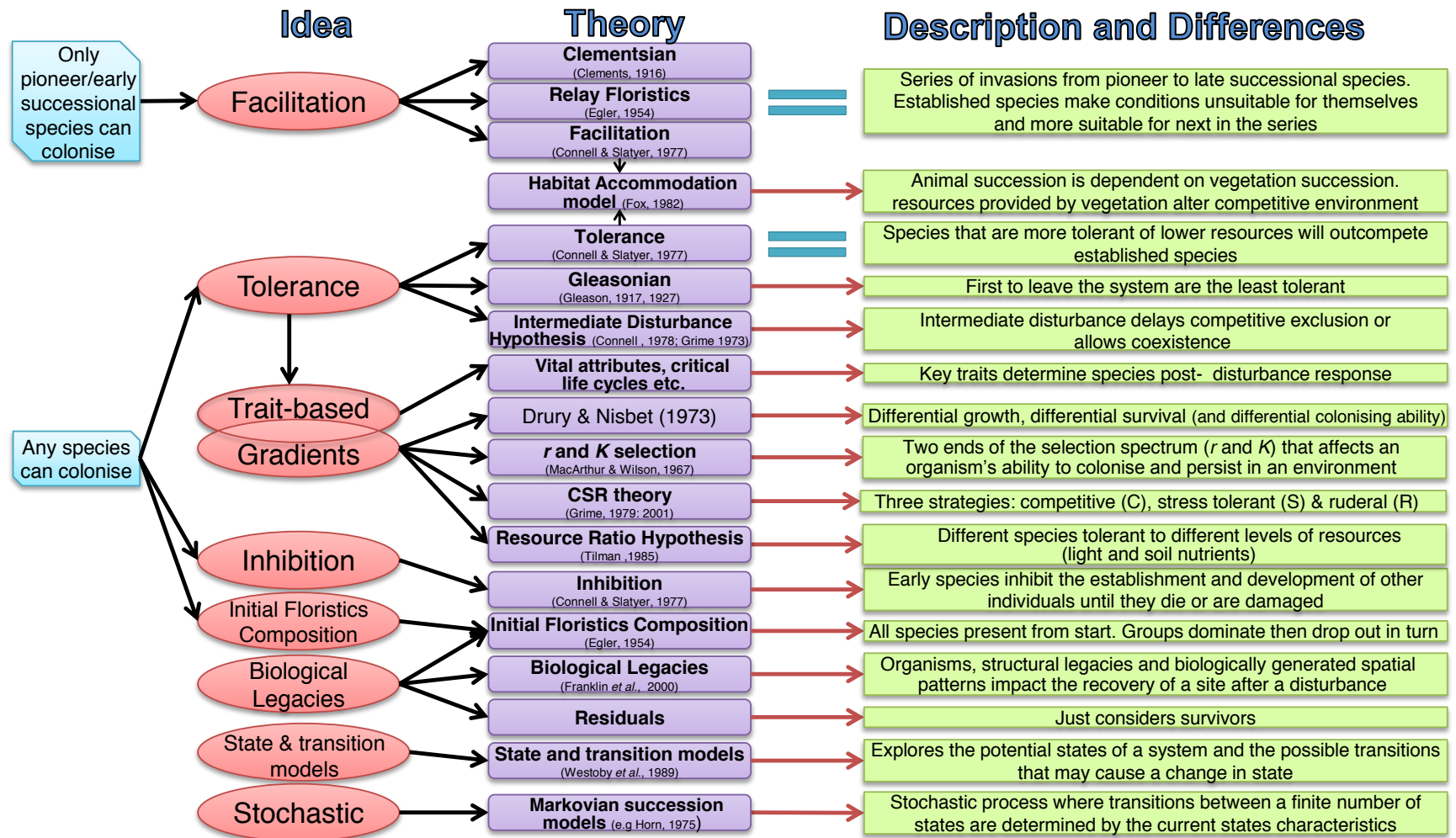
Fig. 5. The relationships between theories on disturbance and succession. Red boxes = key concepts; purple boxes = the theories that use these concepts; green boxes explain the similarities and differences between theories that have a similar idea. Red arrows indicate descriptions that are unique to that theory and the equals signs indicate that the definition is true for all theories that link to the same red oval

(1) Facilitation

An obvious overlap is the concept of facilitation, also known as relay floristics or Clementsian succession (Clements, 1916;Connell & Slatyer, 1977;Egler, 1954). Each of these terms refers to essentially the same idea, i.e. that established species alter conditions so that they are less favourable for themselves and more suitable for the next group of species (Fig. 5). Like other succession models, facilitation describes gradual change, and does not accommodate the idea of punctuated changes (Table 1).

(2) Tolerance

Several theories discuss species' tolerance as a driver of succession. In the Tolerance model of Connell & Slatyer (1977) the important concept is that the intensity of competition increases over time (Table 1). This is similar to Gleasonian succession where the first to leave the system is the least tolerant (i.e. the least competitive) species (Gleason, 1917), a similar mechanism is invoked by the Fugitive species concept (Elton, 1927;Hutchinson, 1951). It contrasts with the mechanism posed by the Habitat Accommodation model (Fox, 1982), where competition changes through time, but does not necessarily increase in intensity (Table 1). Habitat Accommodation is a combination of Facilitation and Tolerance (Fig. 5). The Intermediate Disturbance Hypothesis also could be framed using the tolerance concept. At low levels of disturbance, species most tolerant of strong competition remain. At high levels of disturbance, "tolerance" may be used with a different meaning: tolerance of an extreme abiotic environment rather than an extreme competitive environment. Gradient approaches [e.g. Resource Ratio Hypothesis (Tilman, 1985), CSR theory (Grime, 1979;Grime, 2001) and *r*- and *K*-selection (MacArthur, 1972)] use the concept of tolerance with this second meaning, which is potentially

confusing. A solution may be to reserve 'tolerance' for this second meaning, and use the term 'competition' for the former situation (Connell & Slatyer's (1977) "tolerance" model), where change is brought about by changes in the competitive regime (Table 1).

(3) Traits and gradients

Each of the gradient concepts (e.g. Connell & Slatyer, 1977;Drury & Nisbet, 1973;Gleason, 1917;Gleason, 1927;Grime, 1979;MacArthur & Wilson, 1967;Noble & Slatyer, 1980;Tilman, 1985) emphasises different types of gradients and most include aspects of species' traits (Table 1). For example, Connell & Slatyer's (1977) tolerance model considers species establishment and survival according to their position on a gradient of tolerance to limited resources. By contrast, Tilman's (1985) Resource Ratio hypothesis is very narrowly focused on the gradient of two major limiting resources for plants – nutrients and light [although other work included a wider range of resource gradients (e.g. Tilman, 1980)].

The r- and K-selection concept (MacArthur & Wilson, 1967) and the CSR theory (Grime, 1979;Grime, 2001) (like all gradient theories as noted above) also relate to life-history trait approaches. This is because it is an organism's life-history traits that determine where it resides on these gradients. The main difference between these two theories is that r-and K-selection represents a two-dimensional axis that influences reproductive strategies, while the CSR model has three selection pressures (competition, disturbance and stress) instead of two and was developed only for plants. The Whittaker and Goodman (1979) model provides three similar, but broader, selection pressures to the CSR model. However, the Whittaker & Goodman (1979) model is not easily empirically tested.

The Intermediate Disturbance Hypothesis (Connell, 1978;Grime, 1973) can be mapped onto the

C–R axis of the CSR model (Table 1). In the case of plants, at high levels of disturbance, only

ruderal species will remain, whereas at low levels of disturbance, only highly competitive

species will remain. At intermediate levels of disturbance, there would be a mixture of species

types. However, unlike those successional models that consider the trajectory of community

change following a disturbance [e.g. Initial Floristic Composition (Egler, 1954) and the three

models outlined by Connell and Slatyer (1977)], the Intermediate Disturbance Hypothesis

focuses on predicting species richness given a particular spatial or temporal sequence of

interruptions to succession.

(4) Inhibition and Initial Floristic Composition

The Inhibition model (Connell & Slatyer, 1977) and Initial Floristic Composition theory (Egler,

1954) are similar in two respects. The first is that succession progresses from short-lived species

to long-lived species (Connell & Slatyer, 1977, p. 1123;Egler, 1954). The second is that Initial

Floristic Composition theory also includes the idea that established species vary in their ability to

resist invasion (limited inhibition) (Egler, 1954). Connell & Slatyer (1977) considered that both

the Tolerance and the Inhibition model followed the Initial Floristic Composition model in that

any arriving species can colonise. The main difference between the two theories is that in the

Inhibition model, the first colonisers inhibit the establishment of other species until they die or

are damaged. By contrast, in Initial Floristic Composition, all species are present from the

beginning but different species vary in their dominance at different times in the succession

according to their differential longevity (Table 1). The concept of Initial Floristic Composition

has mostly been applied to abandoned agricultural fields, but the full scope of its application is yet to be ascertained (Table 1).

(5) Biological legacies

Biological legacy theory has some similarities with the concept of Initial Floristic Composition (Egler, 1954) in that the entities that are there from the beginning influence the succession (see Fig. 5). The main difference between the two concepts is that Initial Floristic Composition predicts the specific sequence of vegetation change that will occur through time (Fig. 1B), whereas the biological legacies concept does not. Also, in Initial Floristic Composition, the components leave the system due to differential longevity, while the biological legacy concept does not propose an exit mechanism. The biological legacies concept also includes structural legacies and biologically generated spatial patterns whereas Egler's (1954) model considers only live propagules.

(6) State and transition models

The state and transition concept provides a different approach to many of the earlier succession and disturbance ideas in that it describes situations where there is little change from specific ecosystem states in the absence of disturbance, multiple stable states are possible, and transitions between states can be abrupt (Abensperg-Traun *et al.*, 1996;Westoby *et al.*, 1989). "Climax" communities (Clements, 1916) are stable states, but the key differences from state and transition concepts are that, in the latter, there are multiple states, and that transition from State A to State B does not occur in the absence of a driving disturbance. State and transition models also can

allow for multiple directional changes of ecosystem succession in response to disturbance (Phillips, 2011) and are therefore more complex than linear succession concepts. Trait-based approaches allow similar flexibility in terms of multidirectional change (Table 1).

(7) Summary: relationships between the theories

Although much work on succession and post-disturbance ecosystem recovery has been conducted over the last century, there is no universal disturbance theory that covers all situations and concepts. Many of these different approaches and ideas overlap or use different terms for the same phenomena. To promote understanding of post-disturbance ecosystem recovery, it would be valuable to recognise overlap and redundancy, and attempt to develop a reduced set of terms that more simply defines the range of disturbance-related phenomena. In Section IV, we suggest a framework that describes the phenomena we have reviewed, while purging the redundancy identified in this section (Table 1).

IV. RATIONALISED DISTURBANCE THEORY

As shown in Table 1 and Fig. 5, we have identified a range of unique concepts that should be included in a framework of rationalised disturbance theory. In Fig. 6 we have collated the range of mechanisms through which a community of organisms might transition to another, and we have included the range of ways that gradual change, punctuated change, or no change may occur. Fig. 6 draws together disparate disturbance-related theories into a single framework, showing relationships and interconnections between concepts. For example, three formerly

independently used concepts: Initial Floristic Composition, Biological Legacies and Inhibition are shown to be alternative mechanisms that arise from the biotic and abiotic composition of a community immediately after disturbance (or a change in disturbance regime). A clear example of redundancy is the substantial conceptual overlap of Connell & Slatyer's (1977) Tolerance model with a range of other theories including Gleasonian succession (Gleason, 1917, 1927), the Intermediate Disturbance Hypothesis (Connell, 1978), the Resource Ratio Hypothesis (Tilman, 1985), Fugitive species (Elton, 1927), the Habitat Accommodation model (Fox, 1982) and many gradient hypotheses (Drury & Nisbet, 1973). In Fig. 6 we remove this redundancy, simplifying the set of ecological jargon that ecologists need to consider, while spelling out the full suite of phenomena.

We acknowledge that our approach to synthesis may not fully represent all of the nuances of the original suite of overlapping theories. Nevertheless, the framework can be adapted in future to restore important detail as evidence accumulates, or to expand subsections of Fig. 6, taking a nested, rather than redundant approach.

Much trait-based research is undertaken without reference to succession theory or other mechanisms of community change after disturbance. While species traits can be effectively used to predict changes in community composition (Keith *et al.*, 2007), Fig. 6 illustrates opportunities to identify and communicate better the mechanisms of species responses. By attempting to align the disturbance response of species with particular traits (or communities with particular trait combinations) with other mechanisms of community change like competition and initial composition, there is the potential to discover the circumstances in which some have predictive value, aiding the development of contingent theory (Driscoll & Lindenmayer, 2012). Linking functional groups of taxa with the range of successional pathways illustrated here is a substantial knowledge gap and Fig. 6 provides a framework to allow these concepts to be explored together.

The framework in Fig. 6 should assist future researchers in this field to frame their hypotheses, pose better questions and improve communication between scientists and land managers. We have not specifically discussed the spatial context of post-disturbance succession, although the spatial context can have an important bearing on succession and species richness (e.g. Arthaud *et al.*, 2013;Cadotte, 2007;Östman, Kneitel & Chase, 2006). More work is required to fit the rationalised theory discussed herein into a spatial context. In particular, reconciliation with metacommunity concepts (Leibold *et al.*, 2004) is needed. We noted that neutral metacommunity concepts could drive stochastic community formation (Section II.4). There also are conceptual links between patch-dynamic metacommunities (Leibold *et al.*, 2004), competition-colonisation trade-offs (Turnbull, Rees & Crawley, 1999) and our proposed competition pathways 5 and 7 (Fig. 6) that need to be expanded upon.

We argue that the framework in Fig. 6 has broad heuristic value because it highlights the range of mechanisms and pathways of community change associated with disturbance. Recognising this range of possibilities helps researchers to avoid narrow thinking that can arise when the focus is on just a single theory. The framework can be used to help interpret results from primary case studies, where there are no grounds for assuming a particular mechanism or applying a single theory. The framework can subsequently be used to aid prediction in secondary case studies, where specific components of the model can be tested using a hypothetico-deductive interpretation (Driscoll & Lindenmayer, 2012).
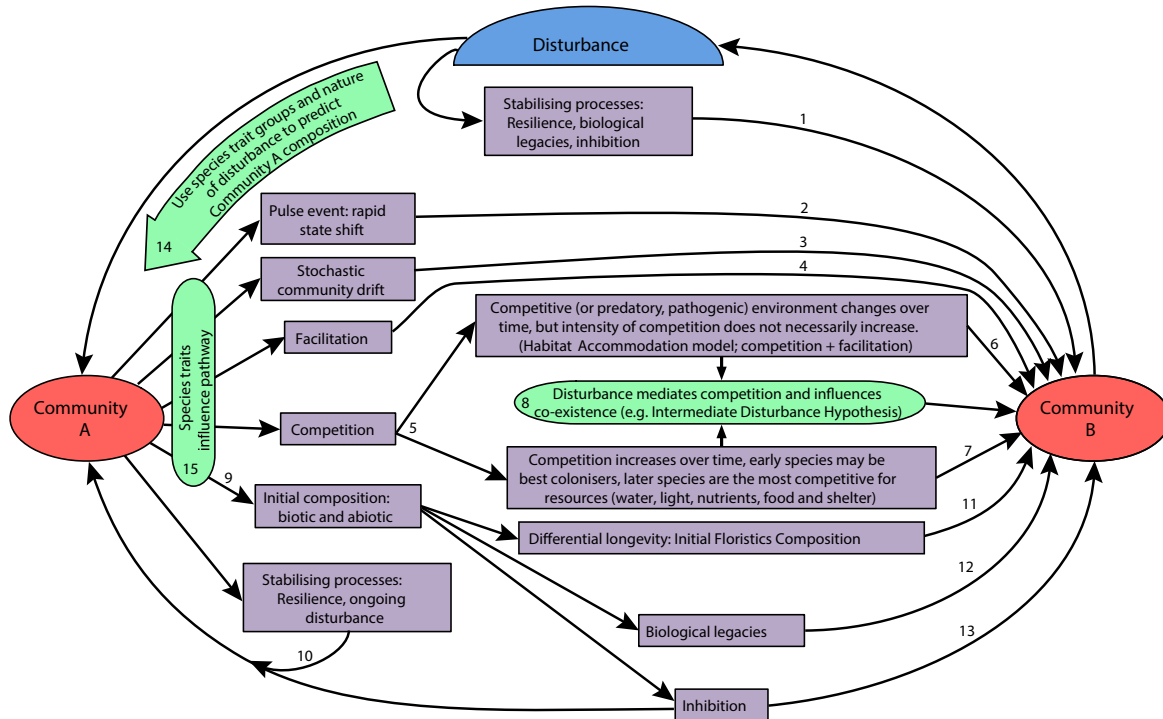
Fig. 6. An integration of the phenomena described by ecological theory related to disturbance. A disturbance (an event, a series, or combination of events) disrupts community 'B'. We use quotation marks to indicate that communities 'A' or 'B' may be, but are not necessarily, the same community at different points in the cycle [acknowledging Cowles' (1901) observation that succession is like 'a variable approaching a variable rather than a constant']. A disturbance in community 'B' may lead to a temporary change followed by recovery, and may be influenced by the effects of biological legacies or inhibition (1). On the other hand, a disturbance could lead to establishment of community 'A' as state and transition theory suggests that a range of alternative states (different communities) is possible, although we illustrate just two states here for simplicity. Succession, neutral, biological legacy and state and transition theories indicate there are a number of possible pathways by which community 'A' may transform into community 'B' after the disturbance. State and transition models suggest there could be a rapid shift between states (2). Neutral theory implies there may be stochastic community drift (3). A range of succession theory suggests that community composition may change through facilitation (4) or competition (tolerance) (5). The competitive environment may change, leading to species turnover throughout the succession, as competition acts in combination with facilitation (6), or the competitive environment may increase leading to a community 'B' consisting of the most competitive species (7). Competitive interactions may be altered by disturbance, and the nature of the disturbance (timing, severity, extent, etc.) can influence the likelihood that species coexist, including for example, circumstances where an intermediate disturbance facilitates coexistence leading to increased species richness (intermediate disturbance hypothesis) (8). Community change may also depend on the initial composition of the community after disturbance (9). Inhibition (or other stabilising processes as emphasised by state and transition models) may maintain community 'A' (10). On the other hand, a new community 'B' may develop through differential longevity (initial floristics composition) (11), or stabilising processes may contribute to the composition of the new community, including effects of biological legacies (12), and inhibition (13). In such cases, other processes primarily drive community change (e.g. 1–8). The composition of community 'A' could potentially be predicted from knowledge of how species with particular traits respond to the disturbance (14). Species traits also likely determine which taxa follow particular pathways between 'A' and 'B' (15). Species traits can be classified in a broad range of ways, including by considering demographic attributes such as where a species occurs on an $r - K$ spectrum or mechanistic approaches that relate disturbance types to traits likely to be affected by that disturbance.

V. CASE STUDY: MOUNTAIN ASH FORESTS IN THE CENTRAL HIGHLANDS OF VICTORIA, AUSTRALIA

We present a case study (Fig. 7), which highlights that many of the phenomena discussed herein can occur conjointly or at different times throughout succession at a site (as demonstrated in Fig. 6 and Table 1). The case study emphasises how the starting conditions and the severity (or type) of disturbance can strongly influence the post-disturbance pathway of an ecosystem. Our case study also highlights the narrow focus that many researchers use when examining post-disturbance ecosystems in that they often consider only one or even no theoretical phenomena and do not consider the full spectrum of theoretical work that might be relevant (e.g. Buddle *et al.*, 2006;Cobb, Langor & Spence, 2007;Duncan, 2006). These problems can limit effective communication among scientists and limit scientific progress.

Our case study uses examples from research in mountain ash (*Eucalyptus regnans* F. Muell.) forests in the Central Highlands of Victoria, Australia. This forest ecosystem provides a useful case study for two main reasons. First, this ecosystem has been subject to long-term studies examining various aspects of forest ecology. Second, different parts of this ecosystem have experienced various levels and types of disturbance (Gill, 1981;Lindenmayer, 2009a). This long-term research, coupled with the existence of disturbance gradients, provides a large body of knowledge on post-disturbance responses in this ecosystem. Other ecosystems could equally illustrate the application of a rationalised approach to disturbance theory, such as the well-studied boreal forests of North America (e.g. see works such as Burton *et al.*, 2003;Heinselman, 1981;Johnson, 1996).

There are three main pathways of post-disturbance succession in the mountain ash forests (Fig. 7), which, in turn, influence the age of the forests and fire intensity (Lindenmayer, 2009a;Mackey *et al.*, 2002). The three pathways illustrate five different disturbance concepts including biological legacies, initial floristic composition, and state transitions (Fig. 7).
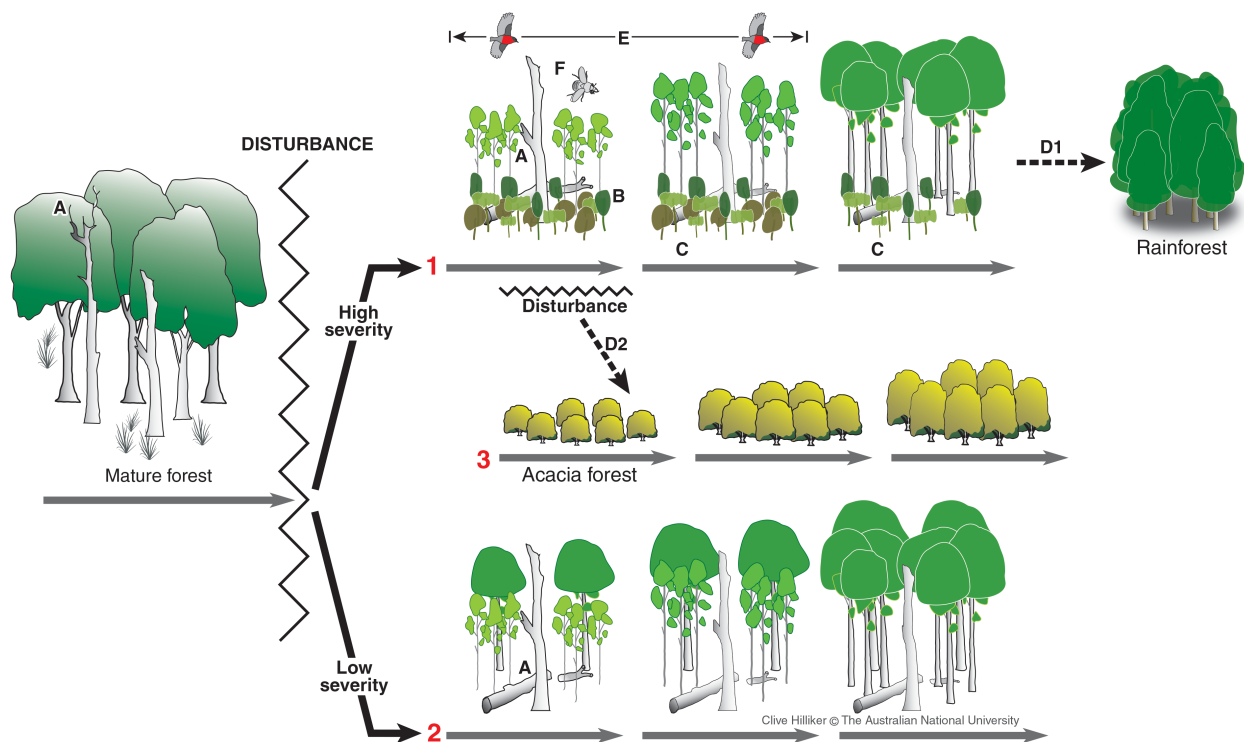
Fig. 7. Diagrammatical representation of the main post-disturbance pathways (1, 2 and 3 as described in the text) and successional theories that have been observed in the mountain ash forests of Victoria, Australia. A, biological legacies: dead trees and logs; B, initial floristics composition: species present from the beginning and becoming dominant according to differential longevity; C, competition (tolerance): the more competitive species will outcompete others; D, state and transition model: D1 – forest transitions from a eucalypt forest to a myrtle-beech-dominated rainforest; D2 – forest transitions from a eucalypt forest to an acacia forest; E, habitat accommodation model: flame robin enters and then leaves the area as habitat changes; F, trait-based approaches: key traits such as dispersal ability (e.g. flight in beetles) can be used to predict species presence at different stages of succession. Note that only relevant aspects of each pathway are depicted.

(1) Pathway 1: mature forest and large infrequent disturbance

The main (and traditionally the only recognised) post-fire pathway in mountain ash forests is mature forest experiencing large, infrequent stand-replacing fires. This produces even-aged stands of the obligate-seeding overstorey tree mountain ash (Ashton, 1981). In old-growth and mature forest, fire promotes a large amount of seed fall from the canopy of mature trees leading to a flush of seedling growth (Lindenmayer, 2009*a*). The vegetation in the mountain ash forest, after an initial fireweed flush, has been observed to follow the Initial Floristic Composition model (with some facilitation occurring that allows new species to enter) for decades afterwards (see B in Fig. 7) (Ashton, 1981). Fire in mature forest also leaves many other biological legacies such as standing dead trees with hollows and large logs (Lindenmayer, 2009a;Lindenmayer & Franklin, 1997). These biological legacies play a very important role in the ecosystem response to the disturbance (see A in Fig. 7) (Lindenmayer, 2009a;Lindenmayer *et al.*, 2012). The presence and abundance of these biological legacies such as logs and dead standing trees will determine the ability of certain species to survive the fire (Lindenmayer, 2009*b*).

Animals also have been observed to follow post-disturbance theories in the mountain ash forests. Shortly after the 2009 fire, previously rare or absent flame robins (*Petroica phoenicea*) appeared in the forests. However, their numbers are expected to decline over time because the vegetation community will become densely structured instead of the open habitat that they prefer (Habitat Accommodation model: see E in Fig. 7) (Lindenmayer *et al.*, 2010). Additionally, a pitfall trap study of beetles two years after the 2009 fires found that the majority of beetles in stands that were burnt were morphospecies with hind wings, while beetles in stands that were not burnt in that fire were predominantly wingless (trait-based approaches: see F in Fig. 7) (Pulsford, 2012).

As time passes since the major disturbance, the understorey of the mountain ash forest can also reveal successional processes at work. More shade-tolerant/competitive understorey species such as hazel pomaderris (*Pomaderris aspera*) and musk daisy bush (*Olearia argophylla*) have been recorded to outcompete the less-shade-tolerant/less-competitive dogwood (*Cassinia aculeata*) [Competition (Tolerance): see C in Fig. 7] (Ashton, 1981).

In a similar mountain ash forest system in Tasmania, Jackson (1968) hypothesised that if the stand was not burnt for 400 years, it would transition into rainforest dominated by myrtle beech [*Nothofagus cunninghamii* (Hook.) Oerst.] (State and Transition model: see D1 in Fig. 7). However, in our central highlands study region, the occurrence of myrtle beech is limited by rainfall and topography, which means that not all stands of mountain ash will transition to myrtle-beech-dominated rainforest (Lindenmayer *et al.*, 2000;Mackey *et al.*, 2002). Stands that do transition to rainforest may continue to be dominated by myrtle beech (Cunningham, 1960).

(2) Pathway 2: mature forest and low severity disturbance

Fires are not always stand-replacing events in mountain ash forests. In response to low- or moderate-severity fire, some trees may survive, leading to multi-aged stands containing biological legacies such as large dead and living trees (see A in Fig. 7) (Ashton, 1976;Lindenmayer, 2009a;McCarthy & Lindenmayer, 1998). Older trees are more likely to survive a moderate-severity fire than younger trees because old trees have thicker bark (Ashton, 1981).

(3) Pathway 3: immature forest

If a young stand of mountain ash forest (less than 25 years old) is burned, few biological legacies remain after the fire. Because the trees are below the age of sexual maturity, there will be limited regeneration and the mountain ash forest may abruptly transition to a different community that is typically dominated by *Acacia* species (State and Transition model: see D2 in Fig. 6) (Ashton, 1981;Lindenmayer, 2009a;Lindenmayer *et al.*, 2011;McCarthy, Malcolm Gill & Lindenmayer, 1999).

VI. CONCLUSIONS

(1) We have attempted to rationalise succession and post-disturbance ecosystem recovery theory. We hope that others will build on our approach, to identify links with other domains of rationalised theory and add components where the framework is incomplete.

(2) In undertaking this review and synthesis, we have brought together a large body of theory into an easy-to-use format, which focuses on unique concepts and discards redundant terms and frameworks. We hope that this rationalised approach to disturbance theory will assist researchers in considering a broad range of theory in planning research, but still allow concentration on specific theories where these have proved important. We also trust that our representation of rationalised theory may be useful for rapid learning about key processes and pathways associated with community change after disturbance.

(3) Despite more than 100 years of research and thinking on the topic of post-disturbance community change, there are still many knowledge gaps (Table 1). The limitations and appropriate uses of some of the theories are yet to be determined or require further investigation. Conversely, because of over 100 years of research and thinking on this topic, the field of ecology

has accumulated a vast array of overlapping and redundant theory, any of which could be used to help frame disturbance research. A rationalised approach to this body of theory cuts through the accumulated concepts, identifying key phenomena and the linkages between them. This provides a framework that can help to identify existing and previously unrecognised knowledge gaps, which we believe could help the field to move forward more efficiently.

VII.   ACKNOWLEDGEMENTS

VIII.   REFERENCES

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