

The Effects of Disturbance and Succession on Wildlife Habitat and Animal Communities

This chapter discusses the study of disturbance and succession as they relate to wildlife. As such, the discussion is confined to those disturbance processes that change the physical attributes of habitat, leading to a postdisturbance trajectory. However, even with this narrowing of the scope of disturbances discussed, there remain formidable obstacles prior to any coherent discussion of disturbance. The first, and most fundamental, is definitional: what constitutes disturbance and succession, and what is habitat? The concepts of disturbance, habitat, and succession are highly scale-dependent; disturbances at one scale become part of continuous processes at a larger scale, and ideas associated with succession require assumptions of constancy, which become highly problematic as spatiotemporal scales increase. Literature on the effects of disturbance and succession on wildlife, however, focuses on a narrow range of spatial scales, primarily occurs within a narrow temporal window immediately following disturbance, and seldom includes interactions between areas within the disturbed patch and the landscape that surrounds it. While these largely descriptive studies undoubtedly have great local value, more general information about the relationships between organisms and environments shaped by disturbance and succession is remarkably limited. Multiple small-scale descriptive studies of the immediate postdisturbance environment do not appear to coherently aggregate into larger understandings of the effects of disturbance and succession on wildlife. Context is important: the conditions at the time of the disturbance, in adjacent undisturbed patches, and within the broader landscape

all affect both the postdisturbance wildlife community and, more importantly, the trajectory of the postdisturbance community. Even for well-studied species, coherent understandings of their relationships to disturbance across time and space are therefore often vague.

Commonly, we look at successional changes in habitat quality by using spatial samples of different ages as if they were a temporal series, which implies spatiotemporal constancy in successional dynamics. This assumption has served wildlife research well, but in the face of directional climate change and the nearly continuous addition of exotic species, this approach is becoming increasingly untenable. We need to embrace the idea that postdisturbance succession is increasingly unlikely to produce communities similar to those that the disturbance altered: short-term successional patterns are likely to be influenced by the large and dynamic pool of exotic plants and animals and longer-term succession by directional climate change.

Together, these observations indicate a need for studies of disturbance and succession at larger spatiotemporal scales. It is, however, important to assess the feasibility of scaling up studies in time and space. Clearly, studies that expand both the spatial and temporal dimensions of data collection quadratically increase costs; longer time frames do not fit into current competitive funding structures and contain a variety of negatives such as the potential loss of data. Broad-scale targeted monitoring, however, can provide a framework allowing acquisition of data at these scales and can be designed to produce both immediate and longer-term results.

Disturbance, Succession, and Questions of Scale

Bormann and Likens (1979) defined disturbance as disruption of the pattern of the ecosystem, principally by external physical forces. This idea, however, assumes that ecosystems function as idealized Newtonian systems, in stasis until external energy is applied. But few ecosystems exist in equilibrium (Sousa 1984). Further, Rykiel (1985) noted that whether disturbance is viewed as changing the state of an ecosystem or being part of that state is entirely a function of scale. At one scale, a tree-fall is a state-altering disturbance; at a larger scale, it is part of a continuous process that creates and maintains the state of an old-forest ecosystem. The same thing is true for larger disturbances; at one scale, fire in western US forests represents a significant disturbance to ecological function, radically altering wildlife habitats. At a larger scale, fire is a part of the ecosystem—many ecosystems are dependent on fire to maintain the presence, patterns, and juxtapositions of plant and animal species (Habeck and Mutch 1973; Covington and Moore 1994; Nowacki and Abrams 2008).

Similar-scale dependencies are associated with the effects of disturbance on wildlife habitat. Habitat is often thought of with a particular scale in mind: perhaps a forest stand or home-range area evaluated across a year or the lifespan of an organism. If successional thinking is applied, habitat may be defined as existing within a specific sere (e.g., a species may be considered to be associated with early seral or late successional forests). However, the habitat requirements for population persistence are, like disturbance, complex and span many scales in both space and time. In space, wildlife habitat spans spatial domains measured in meters (e.g., specific resources for denning), to kilometers (e.g., sufficient resources to support a local viable population), to hundreds of kilometers (e.g., a mosaic of resources and connectivity sufficient to support long-term metapopulation [Levins 1969, 1970] persistence and abundance). Additionally, at all spatial scales, juxtaposition and spatial patterns of habitats are important (e.g., Iverson et al. 1987). Temporally, the definition of *habitat* is even more complex. Again, scales vary from almost instantaneous (e.g., the timing of ice breakup in the Arctic) to millennial (e.g., the processes of erosion and deposition that create soils, caves,

and other habitat features). Temporal habitat patterns are as critical for conservation as are spatial patterns, but much harder to study. In many cases, the events that structure landscapes and define species ranges are rare—often singular. For example, the genetic population structures of many species are strongly associated with glacial vicariance that occurred during the Pleistocene (see Shafer et al. 2010 for a review). To study these rare events, we primarily look to the past to gain insight into their frequency, size, and postevent successional and evolutionary trajectories. Further, for practical reasons, we frequently use habitats of different ages as surrogates for the passage of time, making the tacit assumption that if we were to project one area forward (or backward), it would be similar enough to a surrogate area that we can infer its future or past state by studying that surrogate. I refer to this approach as “trading space for time.”

The study of temporal patterns of habitat over time, and specifically the validity of using spatial surrogates to infer temporal patterns, is tightly linked to the concept of succession. Here I use this term in a neo-Clementsian fashion (Clements 1916; Daubenmire 1952): succession assumes a pattern of orderly and predictable changes in species presence and abundance that occur over time after disturbance, leading to a fairly stable terminal state, or climax. As Gleason (1927) noted, the idea of succession is very appealing: if understood, it allows us to predict the future and to see into the past without needing any data other than what we collect in the present. However, successional concepts cannot be accepted naively. The validity of this concept, and its resulting popularity (or lack thereof), is directly related to the complexity of the system studied and the scale at which the system is evaluated. Simple systems have fewer succession pathways and fewer species; hence, the vegetative trajectories are more predictable. For example, in the western forests of the United States, tree communities are often simple and contain large areas of intact natural vegetative communities. In these systems, succession-based classification systems (e.g., habitat types; Pfister and Arno 1980) and concepts (e.g., potential natural vegetation [PNV]; Küchler 1964) are popular. In highly modified landscapes concepts, however, concepts like PNV become abstract as none of the vegetation within a study area may exist in its putative potential condition (Zerbe 1998). For

these reasons, looked at objectively, succession is often a problematic concept, but one that has proved useful in many communities and without which our ability to study systems and build predictive models would be severely limited. However, regardless of its historical validity, there is good reason to doubt its relevance as a tool to predict future habitat conditions; the likelihood of rapid directional climate change and the increasing presence of exotic species compromise our ability to use past patterns to predict the future. Another concept, community assembly theory, which views communities as being the result of a continuous process of species invasion and extinction (Lodge 1993), may be more germane.

Disturbance and Its Relationship to Wildlife Communities **Defining Disturbance**

The spatial scaling of habitat, including the habitat patch structure generated by disturbance, is ultimately defined by the grain at which specific organisms perceive the world (Kotliar and Wiens 1990) and operationally defined at some arbitrary time scale. Thus, disturbances also are subject to these same scalings: an event that constitutes a significant disturbance for a woodland salamander (e.g., *Ensetina* sp.) may be of little importance to a wolverine (*Gulo gulo*). Thus, when we consider disturbance ecology, we should ideally begin with operational environment of the affected organisms, clearly identify the time frame of interest, and define disturbances accordingly. This, however, is seldom done. When we consider disturbance, we often have a particular scale in mind, generally an intermediate scale. When we label events as disturbances, we envision events such as hurricanes or forest fires and particularly anthropogenic activities such as logging, land clearing, and infrastructure development: scientific articles that claim to study disturbance overwhelmingly study these types of events. However, this scale is not the organism's scale; rather, it is our scale. In part, this is simply a matter of semantics: how we define disturbance rather than what we study. For example, we study the effects of tree-fall and subsequent forest gap dynamics on wildlife; Forsman et al. (2010) found eleven studies of gap effects on forest birds. However, while forest gap formation is an obvious disturbance

process, we discuss and label this process as part of a separate body of literature. Similarly, we are prone to view what we do as being more of a disturbance than what other organisms do. For example, beavers (*Castor canadensis*) instigate a variety of disturbances (tree felling, house and dam construction), oftentimes removing all accessible trees from the area adjacent to their pond (Martell et al. 2006) and thereby creating a shifting pattern of disturbance that can, over many generations, affect large areas (Naiman et al. 1986). However, studies of beaver activity are seldom framed or titled as being disturbance studies.

By choosing to concentrate our studies on mid-scale disturbances, such as fires, and the subsequent changes in habitat, we have, unfortunately, also chosen events that occur at temporal scales that are inconvenient—postdisturbance successional trajectories frequently require many years to evolve. To study these processes, it is therefore necessary either to set up very long-term studies or trade space for time, with its associated assumptions and weaknesses. As noted earlier, trading space for time requires the assumption of a high degree of similarity and transferability across disturbance events and subsequent recoveries. Given these constraints, there are two types of disturbances that occur at scales and with frequencies that allow both study and reasonable transferability: anthropogenic changes such as logging and land conversion, and fires; a great deal of what we identify as the study of disturbance therefore concerns these types of disturbances. Likely for these reasons, and based on practical considerations such as the ease of aging trees and hence inferring past disturbance events, this body of literature has a strong bias toward the study of forested systems.

In addition to often being appropriate in scale, anthropogenic disturbance is highly researchable because we seek to control many aspects of our disturbances. For example, in forestry we apply standardized silvicultural treatments: a clear-cut treatment, in addition to removing all trees, generally will also include removal of residual debris and soil scarification, leaving a fairly homogenous postdisturbance environment that is replicated across multiple treatment areas. Treatment blocks also tend to be of similar size—both economics and policy dictate this. On Forest Service lands in the United States, for example, clear-cut treatments have for many years been limited in size and spacing

to ten to twenty ha blocks interspersed with uncut areas (Franklin and Forman 1987). They also occur at relatively fixed rates across time and space because we desire fairly constant flows of products supplied to a fixed array of mills. Thus, a system of clear-cuts is a much more regularized disturbance pattern than would occur naturally, and for scientific study, these regularizing factors allow us to achieve a level of replication that is generally absent in natural events. Of natural disturbances, fires are probably the most ideal for study. In fire-prone areas, fires occur frequently enough to be grouped based on covariates such as intensity, aspect, and pre-fire vegetation. Thus, fires form another major class of disturbance studies. In addition to these two heavily studied classes of disturbance, a third major group of published studies concerns disturbance events that we perceive as being "natural disasters": hurricanes, floods, tsunamis, and so forth.

Wildlife Studies Associated with Disturbance

Formal studies of the effects of disturbances on wildlife are almost exclusively limited to the immediate aftermath of the event. This phenomenon is perhaps most apparent in the study of natural disasters. For example, a Google Scholar search on "Hurricane Hugo" revealed a total of thirteen journal publications on the hurricane's effects on animals, of which ten (77%) were published within the first five years. However, few studies are currently underway; I was not able to locate a single journal article with animal responses to Hurricane Hugo as the primary subject published after 2002. This pattern is not limited to the study of wildlife: of seventy-two identified journal publications on all subjects concerning the effects of Hurricane Hugo, sixty-seven (83%) were published in the first five years, and none were published after 2008. Given that changes in vegetation wrought by Hugo will affect habitat in various ways for hundreds of years, there is no biological rationale for this spate of studies of the exceedingly ephemeral habitat conditions associated with its immediate aftermath coupled with low levels of interest associated with the still rapidly evolving habitat conditions that currently exist. Further, this pattern—frequent studies immediately after the disturbance followed by

disinterest—is the norm not just for studies of topical natural disasters but is pervasive across disturbance types. As noted by Fontaine and Kennedy (2012), in a recent meta-analysis of fire effects on small mammals and birds, the meta-analysis was limited to short-term (four years or less) responses because data "at longer time scales were too sparse to permit quantitative assessment" (Fontaine and Kennedy 2012, abstract).

ANTHROPOGENIC DISTURBANCE

Within the constraints noted by Fontaine and Kennedy (2012; taxa limited to small mammals and birds and effects to the period immediately following disturbance), there are still hundreds of published papers documenting the effects of anthropogenic disturbance on wildlife. Luckily, there has been a series of recent meta-analyses that provide both syntheses of these papers' findings and extensive bibliographic references. Kalies et al. (2010) performed a meta-analysis of twenty-two papers on the effects of thinning, prescribed burns, and some wildfire on birds and rodents in the American Southwest. Not all species or taxa were equally represented; birds were most commonly studied. Spatial scales were small (less than four hundred ha) and temporally close to the treatment (twenty years or less posttreatment). Ground-foraging birds and rodents showed neutral density responses to the treatments, whereas aerial, tree, and bole-foraging birds had positive or neutral responses to both small-diameter removal and burning treatments but negative responses to overstory removal and wildfire. Hartway and Mills (2012) looked at a variety of anthropogenic treatments to increase nest success, including prescribed burns (nineteen studies, fifty-two species). They also evaluated the effects of livestock exclusion, prescribed burning, removal of predators, and removal of cowbirds (*Molothrus ater*). Of the four treatments, prescribed burning was not the most effective but did significantly increase nest success for most species, though there was a large amount of variation between species groups. Specifically, precocial bird species were negatively affected by prescribed burning. Vanderwel et al. (2007) performed a meta-analysis of the effects of partial cutting on forest birds. All forty-two studies examined the effects of cutting ten years or less after harvest. Of the thirty-four bird species studied, fourteen declined with increasing har-

vest intensity and six increased. Not surprisingly, deep forest birds such as ovenbirds (*Seiurus aurocapilla*) and brown creepers (*Certhia americana*) were the species most sensitive to harvesting.

FIRE

Similar to anthropogenic disturbances, a number of recent meta-analyses document the effects of fire on wildlife. Not all of these meta-analyses separate natural fire from anthropogenic treatments such as thinning or prescribed burns. For example, Zwolak (2009) performed a meta-analysis of fire clear-cutting and partial cutting on small mammal populations. Of the fifty-six studies used in the meta-analysis, most (fifty-four) documented short-term changes. Only eleven documented longer-term (ten to twenty years after the disturbance) effects (Zwolak 2009, supplemental, appendix A). Zwolak found that deer mice (*Peromyscus maniculatus*) increased and red-backed voles (*Myodes gapperi*) decreased after disturbance, with the effect size increasing with rising disturbance intensity. These patterns relaxed as time since disturbance increased. Fontaine and Kennedy (2012) performed a meta-analysis of forty-one papers, documenting the short-term effects of fire and fire surrogates on small mammals and birds. They, like Zwolak (2009), found that postdisturbance effects on the abundance of species increased with increasing fire severity. A total of 119 bird species and 17 small mammal species were analyzed by Fontaine and Kennedy (2012). While generalizations across this broad of a group are difficult, in many ways their results mirror those of Vanderwel et al. (2007) and Zwolak (2009): the largest positive effect was on deer mice in severe burns whereas forest birds such as ovenbirds and hermit thrush (*Catharus guttatus*) were negatively affected. Interestingly, brown creepers were positively affected by moderate intensity disturbances. While the period immediately following disturbance may exhibit the most profound shifts in structure and composition with a relaxation toward the predisturbance state over time (e.g., Zwolak 2009), this is not always the case. Hossack et al. (2013), studying salamander response to fire in Montana, found little change in abundance during the period immediately after wildfire but significant declines seven to twenty-one years after disturbance. Because we lack very many long-term studies, the gen-

erality of the pattern observed by Hossack et al. (2013) is unknown.

General Strengths and Weaknesses of Disturbance-Related Meta-analyses

Throughout these meta-analyses, a general pattern emerges: bird response to disturbance is much more heavily studied than is mammal response—confining their scope to the effects of fire alone, Leidolf and Bissonette (2009) identify 512 studies on birds—and mammal study is almost exclusively limited to small mammals. The general paucity of habitat disturbance studies for mammals other than small mammals is likely due to several factors. Perhaps the most critical factor is that for larger mammals, home range sizes and/or densities are not compatible with abundance estimation within disturbance classes. Another is that they are far more difficult to locate and count than are small mammals and particularly birds. Even for small mammals, there is no approach that provides as efficient an estimate of occurrence and relative abundance as a bird point-count. Thus, specific disturbance studies of many mammalian species of interest such as large carnivores are impeded both by the utilization of large areas that likely exceed areas of disturbance and difficulties in obtaining sufficient sample sizes. The effects of disturbance on other groups such as herpetofauna are far less studied.

In addition to being limited in types of species analyzed, meta-analyses are weakened by the need to reduce studies to groups that can be evaluated based on a common metric (effect size) and common covariates such as time since disturbance. While such grouping is necessary, all disturbances are not created equal; postdisturbance abundances may be correlated with abundances within the general landscape (e.g., Brotons et al. 2005), a covariate that is generally missing from disturbance studies. Similarly, the effects of past disturbances may have altered systems leading to different responses to the studied disturbance when viewed across many systems. Fox (2011), for example, notes that dry, disturbance-prone grasslands generically have fewer granivores than other grasslands; these systems would therefore be expected to have different responses to any specific fire because they are already adapted to the oc-

currence of frequent fires. Assuming that a species can persist through a disturbance and within the immediate postdisturbance landscape, likely the postdisturbance vegetative trajectory is more important than the time since disturbance. Monamy and Fox (2000), for example, found that recolonization trajectories for an old forest specialist differed between two fires based on time since disturbance but that the two trajectories were concordant when vegetative trajectory rather than time was evaluated. This pattern appears logical and is likely general. If this is the case, then standard approaches to successional studies where time since disturbance is used to characterize organism response are likely produce weaker results than studies that measure vegetative conditions directly.

Bird Studies Where Evaluation Close to the Disturbance Event is Essential

Clearly, more common and replicable sorts of disturbance, like fire, will be more likely to engender meaningful adaptations. However, even for common disturbance types, such as fire in dry environments, immediate postfire conditions will be relatively rare on the landscape. To take advantage of these conditions, population responses must be quick and the organisms need either to be common enough to be on or adjacent to the fire when it occurs or to be mobile enough to find these disturbances quickly so as to take advantage of the ephemeral postdisturbance environment. It is not surprising that, for example, deer mice show large increases in postfire environments. They are generalists and therefore present in the area, can reproduce rapidly, and normally favor bare areas over dense grass (Pearson et al. 2001) and should therefore prosper in postfire environments. Similarly, avian species, being highly mobile, can locate desired environments including recent disturbances and can evolve to take advantage of these conditions. For these reasons, the study of avifauna in postfire environments is both active and biologically appropriate. Saab and Powell (2005), in a review of literature on over two hundred species of birds and their associations with fire, showed that aerial, ground, and bark insectivores clearly favored recently burned habitats whereas foliage gleaners preferred unburned habitats. As with other studies, virtually all of the associated papers evaluated effects within

the first five years after the burn. However, unlike other taxa, some bird species are specifically adapted to these immediate postfire conditions, making their study in these environments especially useful. Notable among the bark insectivores is the black-backed woodpecker (*Picoides arcticus*). This species colonizes burned areas within one year after a fire, occupies burned areas for three to five years, and peaks in density around three years after fire (Caton 1996; Saab et al. 2007). Outside of this window, when postfire environments are optimal, black-backed woodpeckers are difficult to locate and are distributed diffusely feeding, opportunistically, on recently killed trees (Tremblay et al. 2010, Dudley et al. 2012).

Succession Defining Succession

Succession is an idea that emerged in the late 1800s and was championed by Clements (1916). He envisioned the process as an orderly series of plant assemblages from the point of initiation through to the "climax," a stable state. Just as we define disturbance as events that we find disturbing given our viewpoint, similarly, we tend to consider succession in terms of processes that scale reasonably to our lifetimes. For these reasons, the genesis of succession as a concept began with the observations of the dynamics of forests (Clements 1916) and is most commonly still evoked in this context. A great deal of thinking about this concept has occurred since Clements wrote "Plant Succession: An Analysis of the Development of Vegetation" in 1916, but the underlying ideas have remained remarkably stable. Primarily, the concept has been embellished, incorporating ideas such as "secondary" succession, in which initiation contains elements of the predisturbance ecosystem, and various "disclimaxes," where an area is prevented from evolving into its presumed true climax by processes such as frequent disturbance or grazing (see Meeker and Merkel 1984 for a discussion). As mentioned previously, succession has retained popularity in many fields, particularly where ecosystems are simple and primarily composed of native species. Even in these simple systems, however, there is a great deal of variability in these trajectories due to the effects of pathogens and increasingly due to novel weather patterns owing to climate change. For

example, Rehfeldt et al. (2009) showed that historically novel weather patterns, but patterns that are predicted to become increasingly common in the future, immediately preceded major aspen (*Populus tremuloides*) die-offs in Colorado.

One critical aspect of successional thinking is that, although the initiation conditions might vary as would, to a certain extent, the trajectory toward climax conditions, the climax conditions are invariant. As Horn (1975) noted, an invariant steady state is a property of stochastic systems with constant transition probabilities (Markov chains). Usher (1979) observed that if succession is described as a Markov process, then transition probabilities are likely not constant and will be affected by many factors such as population processes. Cadenasso et al. (2002), for example, showed that levels of mammal herbivory play a key role in early successional trajectories of old fields. With many exotic species entering ecosystems, the probability of unforeseen biological feedback obviously increases. For example, the successional trajectories of western North American grasslands to disturbance have been radically altered by the introduction of a plethora of exotic plant species. In western Montana, spotted knapweed (*Centaurea maculosa*) has occupied vast areas to the detriment of both native bunch grasses and native forbs (Callaway et al. 1999). In an effort to control knapweed, exotic gall flies were introduced. They failed to control the knapweed but instead became superabundant, leading to a variety of secondary trajectories involving increased densities of deer mice and associated hantavirus (Pearson and Callaway 2006). These grass systems continue to be inundated by new exotics (e.g., leafy spurge [*Euphorbia esula*]) and with climate change, other species, such as yellow star-thistle (*Centaurea solstitialis*), common in adjacent states, may gain foothold.

For a system to move in an orderly manner from disturbance toward a steady-state climax, both the species involved and the climatic background need to remain constant. This strong requirement for constancy was first challenged by Gleason (1927), who argued that a plethora of factors lead to unique postdisturbance trajectories. In the eighty-three years that have elapsed since Gleason's paper was published, the use and acceptance of successional concepts has split along disciplinary lines: disciplines like phylogeography that evaluate

phenomena across broad scales of space and time are necessarily Gleasonian, whereas fields that study small, local phenomena tend to be Clemensian (Hortal et al. 2012). The effects of rapid directional climate change on this debate are to shrink the spatiotemporal domain across which constancy is a reasonable conceit. We are relatively sure that climates will change significantly over the next several centuries and that climate change is already affecting ecosystems, but our understandings of both the details of local climate change and, even more critically, the effects of these changes on habitat and the wildlife that these habitats support are vague (Walther et al. 2002). This uncertainty is obviously increased by the continuous entry of additional exotic species whose interactions with current ecosystems are largely unknown. There is a school of thought that believes that these specifics, when taken together, are important enough to render the entire concept of succession suspect (Ricklefs 2008).

Wildlife Research on the Effects of Succession

The overwhelming number of disturbance papers that measure immediate postdisturbance responses and the associated lack of longer-term studies dictates that the direct study of the site-level effects of succession are sparse to nonexistent. One of the few cases where long-term studies on primary successional dynamics are ongoing is within the area affected by the pyroclastic explosion of Mount Saint Helens (e.g., Spear et al. 2012). Because large-scale population-level studies of the effects of succession on wildlife are difficult and seldom done, most of our understandings of forest succession on wildlife are associated with habitat use data. For example, we know that some species have strong associations with certain habitats and that these habitats are related to disturbance. The Florida sand skink (*Plestiodon reynoldsi*), for example, is obligately associated with Florida scrub habitat (Schrey et al. 2011), a cover type that requires high-intensity fire on a five-to-eighty-year time scale (Laessle 1958). Knowing this habitat association, we can infer the relationship between this species and succession. Given this constraint—that we understand habitat relationships and know the disturbance regime associated with a particular vegetative community—there is a vast lit-

erature on the effects of succession on wildlife (see Hunter and Schmiegelow 2011 for a recent review). Interestingly, a great deal of this work focuses on the two ends of the successional spectrum: early successional conditions associated with the immediate aftermath of disturbances and the study of a variety of organisms that are dependent on old forests. This may be because organisms of interest are associated with these two seres. For ungulates, likely the most heavily studied mammal group, the general understanding is that early seral environments are preferred due to both the encouragement of forage and increased forage nutritional content (e.g., Hobbs and Spowart 1984), and a great deal of focus is therefore on the generation and maintenance of these conditions. Similarly, because very old forests are in decline worldwide, dependent species often follow this trend and may become endangered. Species such as the spotted owl (*Strix occidentalis*) and red-cockaded woodpecker (*Picoides borealis*) have become iconic in this regard (Bart and Forsman 1992; Ligon et al. 1986). These older forests are not only in decline but often are associated with higher levels of biological diversity when compared to earlier seres (e.g., Díaz et al. 2005). The emphasis on early seral and old growth forests is also due to a perceived overabundance of mid-aged forests owing to a variety of human activities. Under natural disturbance regimes, forest age structures frequently follow negative exponential or Weibull distributions (Van Wagner 1978), or distributions containing significant areas of both old forest and areas that have recently been disturbed. Conversely, human-caused disturbance generally leads to truncated age distributions and can simultaneously decrease early seral conditions through activities such as fire suppression (e.g., Betts et al. 2010).

Disturbance Viewed in a Landscape Context: Studies of Both Disturbance and Succession

In the case of black-backed woodpeckers, postfire conditions are clearly essential habitat, but for many other species these environments are rare and noncritical. However that may be, based on this review, it is clear that targeted studies of disturbance occur almost exclusively during the immediate aftermath of the event. While it is clear that this has been our approach, it is

reasonable to ask whether it is a necessary approach. We could, rather than seek to quantify the specific effects of specific disturbances, endeavor to design studies that would allow comparison and generality between disturbances. In the case of hurricanes on the eastern coast of the United States, for example, rather than studying the effects of Hugo, one could ask how much the immediate postdisturbance conditions related to Hugo resemble those of other recent strong "Cape Verde-type" hurricanes that made landfall on the southeastern coast of the United States (e.g., Fran [1996]; Floyd [1998]; Isabel [2003]). One paper, Rittenhouse et al. (2010), attempted to place the effects of hurricanes in a broader context, including both immediate poststorm effects and overall changes in species composition for birds. Rittenhouse used the North American Breeding Bird Survey (BBS; Link and Sauer 1998) to infer species abundance patterns for the period 1967–2005. This period included a number of hurricane landfalls, notably Hurricane Hugo (September 1989). Study areas were chosen based on the intersection of hurricane tracks and a time series of annual or biennial satellite imagery. The main effect of hurricanes was seen in the year immediately following the hurricane, where modest decreases in abundance and increases in species richness were similar across focal areas. Interestingly, although hurricanes caused a threefold increase in the extent of disturbed forest within the focal areas, this factor was associated with changes in community similarity for only three of the thirteen avian groups examined and was not associated with patterns of avian abundance or species richness. Rittenhouse et al. (2010) attribute the lack of relationships between disturbance levels and population responses to landscape scale heterogeneity; refuges were present in areas where intact forests were the pre-disturbance land cover. This understanding is similar to that of Brotons et al. (2005), who found that local abundances in areas exterior to disturbances affected postdisturbance abundances within the disturbed area. Thus, to understand postdisturbance trajectories, evaluating the larger landscape may be essential. While Rittenhouse et al. (2010) were able to analyze data at spatial and temporal scales sufficient to infer generalized relationships, studying disturbances at this scale is difficult and was only possible in this case because of the presence of the BBS, which is relatively unique

both in its longevity and in its spatially comprehensive-ness. However, even though Rittenhouse et al. (2010) were able to apply forty years of BBS data, because hurricanes occurred sequentially within the time period, statistical statements were limited to a period within ten years after disturbance.

A rare example of a meta-analysis of both disturbance and succession is found in Schieck and Song (2006). They performed a meta-analysis of studies on boreal forest birds for a period of 0–125 years after disturbance. Interestingly, they found that while bird communities changed after a disturbance, composition changes were largely associated with numbers of occurrences rather than actual changes in species composition. All species with measurable counts (greater than five) were present in all forest types. The ability of organisms to persist in all forest types and conditions obviates the need to colonize areas except for after the most extreme events. It also suggests that immediate postfire abundance studies may not provide informative data on the landscape-level responses of populations to disturbance and succession.

Species Relationships to Disturbance and Succession: The Case of the Spotted Owl

Given the current approach of conducting largely independent and descriptive studies of postdisturbance organism response, it is reasonable to ask how well these studies composite into generalized understandings for any organism. The spotted owl, being one of the most heavily studied species, provides a good example of the difficulties associated with determining the relationships between an organism and disturbance while applying this methodology. As mentioned previously, the spotted owl has become an iconic organism representing an old forest obligate (Bart and Forsman 1992), and for this reason, the long-term viability of owls in fire-prone forests has been questioned (Spies et al. 2006). However, spotted owls exist in a wide variety of forests, including some that are highly modified (Thome et al. 1999). Short-term relationships to anthropogenic disturbance have been highly studied, with uniformly negative relationships (e.g., Forsman et al. 1984; Franklin et al. 2000), except where the dominant prey are woodrats (*Neotoma fuscipes*; Thome et al. 1999). Fire is much less heavily studied, and the effects are less

clear. In some cases, low-severity fire appears to have little effect (Roberts et al. 2011). Clark et al. (2013) associated negative effects with fire, but sites they studied had been burned and salvage logged, and pre-fire timber harvest had occurred. Due to sample size constraints, Clark et al. (2013) could not separate anthropogenic and natural disturbance factors. Further, while Franklin et al. (2000) found short-term negative effects, the heterogeneous fire-generated landscape of northwestern California featured high reproductive and survival rates (Franklin et al. 2000)—the fire mosaic in general appeared to produce excellent owl habitat. In short, the relationship between spotted owls and disturbance is complex and our understandings are still very nebulous. Using derived information to conserve spotted owls into the future is also complicated by the twin factors of climate change and exotic species introduction. Owl demographics are sensitive both to regional climate and local weather (Glenn et al. 2010). Further, fire frequency is anticipated to increase in the Pacific Northwest with climate change (McKenzie et al. 2004). Lastly, the invasion of the barred owl (*Strix varia*) is having a profound negative effect on spotted owl demographics across its range (Dugger et al. 2011), fundamentally changing the expected population responses to specific vegetative patterns. In short, the spotted owl provides a case study in all of the complexities highlighted in this paper. The effects of disturbance are complex, depending both on time since disturbance and the scale at which the question is asked. Effects of any specific type of disturbance are difficult to quantify because, at the scale of spotted owl home ranges, a variety of disturbance types have often occurred: fire, logging, and postfire salvage. Lastly, our understandings concerning the effects of postdisturbance succession on the quality of spotted owl habitat have been fundamentally altered by the invasion of an exotic competitor.

Approaches to the Problem

It is clear that our traditional approaches, involving primarily small-scale, short-duration descriptive studies within disturbed areas (and sometimes including undisturbed control areas), while producing much knowledge of local importance, do not provide a coherent approach to increasing our knowledge of the

more general effects of disturbance and succession on wildlife. It is equally clear that the traditional approach of trading space for time to study succession is becoming less and less tenable due to the increasing pool of exotic organisms and the directional nature of climate change. What is less clear is how to move forward in a manner that leads to more rapid increases in our knowledge of these processes while existing in a world that is in a rapid state of biological flux. The simple answer is to expand our studies in both space and time. This would allow the formalization of the context in which disturbance occurs, including the effects of landscape pattern and habitat juxtaposition, and would avoid invoking constancy assumptions to infer future states. There are, however, major problems associated with this approach. The first is cost. Increasing the size and duration of a study quadratically increases the costs. Further, funding large, long-term projects is difficult given the competitive grant paradigm under which a large proportion of science is funded. Competitive grants generally have both spending and time limits that preclude their direct utility for long-term funding; long-term studies are often patched together by acquiring multiple grants, often from different sources. Additionally, there are many ways that these programs can fail and many examples of historical failures due to funding drying up, data loss due to inadequate archiving, failures to maintain quality control across time and space, and poor initial designs leading to the collection of large quantities of relatively useless data. Lastly, there is the strong, but often unacknowledged, power of serendipity associated with many independent studies. The ability to capture serendipity is decreased if scientific resources divert from a large number of small, highly independent studies and commit to a small number of highly directed, long-term projects.

There are, however, approaches that merge the fields of science and monitoring and which may prove useful in documenting landscape-level changes associated with disturbance and subsequent succession. Targeted monitoring (Yoccoz et al. 2001; Nichols and Williams 2006) combines principles of scientific design including clearly articulated goals and specified error levels with the large-scale, long-term requirements for biological monitoring. Increasing the proportion of monitoring that is specifically targeted could allow a reallocation of extant long-term funding into efforts to

collect appropriate data to assess biological processes across broader spatiotemporal domains. Because of the high level of scientific design associated with targeted monitoring, intermediate short-term products can both increase the immediate utility of the monitoring and provide feedback on its overall efficacy. Secondly, monitoring efforts should take advantage of new technologies and, specifically, genetic sampling (Schwartz et al. 2007). Not only do these methods often provide the least expensive approach to sampling species (e.g., Kendall and McKelvey 2008), but genetic data are nearly unique in that, if the samples are retained, these samples can be reanalyzed at a later date. Even without the formal retention of genetic data, the past collection of materials that contain genetic data has allowed retrospective studies of populations. For example, Miller and Waits (2003) were able to retrospectively calculate the effective population size of grizzly bears in Yellowstone National Park by analyzing 110 museum specimens collected between 1912 and 1981. Because of this ability to retrospectively analyze data collected in the past, genetically based monitoring is less dependent on current technologies than are most other monitoring approaches. With genetic data, new technologies can be applied to extant samples, allowing a fully modern analysis of all data regardless of collection time. This ability also provides a safeguard against data loss and allows post-hoc testing quality controls: assays can be repeated both to recover data and to ensure that the original analyses were correct.

Conclusions

There has been little to no attempt in the literature to view disturbance in terms of the operational environment of the studied species; we define disturbances at anthropocentric scales. While this is biologically problematic, it is so ubiquitous that it is impossible to write a review article without also adopting this conceit. However, given this constraint, there is a vast body of literature associated with both the effects of disturbance and succession on wildlife. However, due both to practicalities and interest levels, the vast majority of specific studies on the effects of disturbance focus on the period immediately postdisturbance; few studies extend beyond five years postdisturbance. Further, most studies are small in scope and are not designed to

test concepts; most generalizations are based on compositing these small-scale primary studies through literature reviews and meta-analyses, of which there are many. However, as the case of the spotted owl demonstrates, it is difficult, even with many largely unrelated small-scale studies of specific areas, to generate coherent understandings of general relationships between an organism and its disturbance environment. Successional studies generally trade space for time, assuming that patterns associated with older habitats generated by past disturbances will indicate future patterns in newly disturbed areas. While this practice is directly related to the paucity of longer-term disturbance-related studies, it is also a necessity as many of the successional processes we care about occur across hundreds of years. This approach has historically proven to be extremely useful, but it contains a variety of hidden assumptions that are unlikely to be met as the rate of biological change increases worldwide.

We are currently seeing forest mortality at levels unprecedented in recent history (Allen et al. 2010). These large-scale disturbances provide the opportunity for ecosystems to evolve to meet climatic exigencies and are the engine of predicted broad-scale biome shifts. Given this, we should not assume that relationships based in large part on disturbance events in the past will necessarily provide adequate guidance when predicting the ecological trajectories associated with current processes.

Rittenhouse et al. (2010) demonstrated that the utility of broad-scale temporally stable monitoring for evaluating the effects of disturbance on wildlife communities and monitoring efforts such as BBS will most likely become increasingly important as climate change and exotic species produce increasingly novel ecosystems (Hobbs et al. 2009); we should support these efforts and seek to increase the number of taxa that are monitored. However, these sorts of generalized surveys will always be weak for evaluating specifics of disturbance and succession. Given the pivotal role disturbance plays in ecological change, more specific focus is probably warranted. To meet this need, we can design targeted monitoring studies specifically designed to assess the effects of disturbance and succession on wildlife populations. Ideally, these would represent a redirection of existing monitoring efforts, allowing us to ascertain whether successional trajectories and as-

sociated wildlife communities were following expectations as well as when and where systems were changing in unexpected ways.

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