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CONCEPTS & THEORY

Ecological consequences of compound disturbances in forest ecosystems: a systematic review

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Abstract. Investigations of compound disturbances that alter forest resilience (i.e., recovery time or trajectory) have escalated over the past two decades. We used a systematic approach to identify and describe the ecological consequences of discrete forest disturbance events involved in compound interactions. Fire, wind disturbance, and salvage logging were the most common disturbance types investigated. Most compound interactions occurred in North America and involved five or fewer years between disturbances. Common and interrelated disturbance legacies that facilitated compound interactions included reduced seed source availability, deadwood deposition and extraction, and increased light and growing space availability. Forest recovery was assessed with a diversity of metrics including woody and herbaceous plants, soil properties, and carbon stocks, which sometimes determined whether and what kind of compound interaction was detected. Distinctions between recovery time and trajectory, forest succession and development, and species-specific and community-level responses also influenced the detection and direction of compound interactions. Moving forward, we advocate a more holistic approach to quantify ecosystem recovery that considers multiple response variables. Other opportunities to improve compound disturbance ecology include increased emphasis on understudied disturbance types, regions, and forest types. We also encourage more research on buffering interactions that increase forest resilience, which were underrepresented in this review.

Key words: biological legacies; disturbance interactions; ecological theory; linked interactions; multiple disturbances; perturbations; recovery; repeated disturbances; resilience; resistance; structure; succession.

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INTRODUCTION

Disturbances modify forest composition, structure, and function, and leave legacies that impact the rate and trajectory of forest recovery (Oliver and Larson 1996, Franklin et al. 2002). Natural disturbances include biotic events, such as insect outbreaks and invasive pathogens, and abiotic events, such as fires, floods, ice storms, and damaging wind events. Forest succession and development are also directed by human impacts that range from exploitative logging and land-use change to deliberate silvicultural entries designed to achieve desired conditions. The widespread occurrence of more frequent and severe natural disturbances has been attributed, in part, to precipitation and temperature anomalies associated with global change (Dale et al. 2001, Seidl et al. 2017, Sommerfeld et al. 2018). Coupled with growing human demands, recognition of altered disturbance regimes has motivated interest in multiple interacting disturbances (Turner 2010, Buma 2015). Interacting disturbances may cause unexpected rates and trajectories of forest recovery and reduce resistance and resilience to future perturbations (Paine et al. 1998, Bigler et al. 2005). Understanding disturbance interactions is therefore critical to forecast changes in ecosystem properties and implement management strategies.

Buma (2015) distinguished two types of disturbance interactions: linked and compound (sensu Simard et al. 2011). Linked interactions alter forest resistance (i.e., capacity to endure disturbance without changing), and compound interactions alter forest resilience (i.e., capacity to recover to pre-disturbance conditions; Cannon et al. 2017). Forest resilience includes engineering resilience, which is inversely related to recovery time, and ecological resilience, which describes the amount of energy required to direct recovery toward an alternative state (Holling 1973, Angeler and Allen 2016). Thus, linked interactions describe the influence of one disturbance on forest response to (i.e., resistance to) another disturbance, and compound interactions describe the combined effects of multiple disturbances on altering the rate or trajectory of forest recovery (Paine et al. 1998, Simard et al. 2011). Interacting disturbances are also defined by whether resistance and/or resilience are decreased or increased (Cannon et al. 2017, Kane et al. 2017). When one disturbance enhances the impact of another by decreasing resistance or resilience, the interaction is amplifying. Alternatively, buffering interactions describe situations when one disturbance reduces the impact of another by increasing resistance or resilience (Cannon et al. 2019).

Disturbance interaction mechanisms are mediated by disturbance legacies, which include changes in the spatial arrangement of physical site conditions and life-history strategies represented by residual organisms and propagules (Franklin et al. 2000, Johnstone et al. 2016). For example, in one of six vignettes used to formalize the compound disturbance concept, Paine et al. (1998) described how ash deposits from a volcanic eruption thinned native vegetation in Hawaii Volcanoes National Park. Volcanic legacies, including ash deposits and reduced vegetation cover, facilitated invasion of an exotic plant that grows faster than natives, yields abundant seed, and fixes high levels of nitrogen that is incorporated in the soil (Vitousek and Walker 1989, Vitousek 1990). Thus, the eruption reduced resistance to the invasion (a linked interaction), which altered post-eruption successional trajectories and nutrient dynamics (a compound interaction).

Though identification of linked interactions is possible during or soon after the disturbance events of interest, impacts of compound disturbances take longer to manifest. Forest recovery is a continuous process, and initial post-disturbance conditions may not indicate long-term recovery trajectories (Gill et al. 2017). Despite theoretical advances to describe changing disturbance regimes and alternative states, quantification of ecosystem resilience remains a tenuous task from an operational perspective (Seidl et al. 2016). Moreover, determination of whether disturbances impact resilience can depend on which response variables are considered (Carpenter et al. 2001).

The goal of this review is to identify and describe the ecological consequences of compound forest disturbances. A systematic review of the literature is used to create a catalog of disturbance combinations and compare them based on different manifestations of compound interactions. Although forest recovery can be assessed with a diversity of response variables, limited use of these metrics restricts understanding of disturbance impacts. As such, we are particularly interested in how compound disturbances are quantified, and how the consideration of different response variables influences how compound interactions are identified and described. Compound disturbances are also compared by geographic regions and forest types, and disturbance legacies and mechanisms of change (Peters et al. 2011). This review provides a framework for future investigations and, by identifying generalities in the literature, improves our ability to define, forecast, and manage for compound disturbances.

METHODS

Article selection

A keyword-driven approach was used to search the Web of Science Core Collection database with the terms: (“compound* disturbance$” OR “compound* perturbation$” OR “disturbance interaction$” OR “interacting disturbance$” OR “multiple disturbance$” OR “multiple perturbation$” OR “repeat* disturbance$”) AND (forest OR savanna OR woodland). This search yielded 328 records published through April 2019, which were screened and assessed for eligibility (Fig. 1; Moher et al. 2009). After database searching, identified records were vetted by titles, abstracts, and keywords to remove those that did not match the focus of this investigation. Specifically, 40 records were excluded that did not pertain to forest ecosystems and/or used the terms compound, interacting, multiple, or repeat to refer to something other than multiple disturbance events (e.g., organic compound). After screening, 288 articles remained that referred to multiple forest disturbances (Appendix S1). The full texts of these articles were reviewed to exclude those that did not meet eligibility criteria for inclusion in the review framework. Excluded articles consisted of review papers and short communications, studies focused on non-discrete disturbances such as climate change and chronic herbivory, disturbance reconstructions, and those that did not measure post-disturbance recovery with empirical data (e.g., prospective simulation models). After eligibility assessment, 59 full-length research articles remained that used empirical data to measure forest recovery after multiple, discrete, disturbance events with overlapping spatial distributions. These articles were included in a review framework designed to compare disturbance combinations by forest types and locations, disturbance types and timing, and attributes of disturbance interactions.

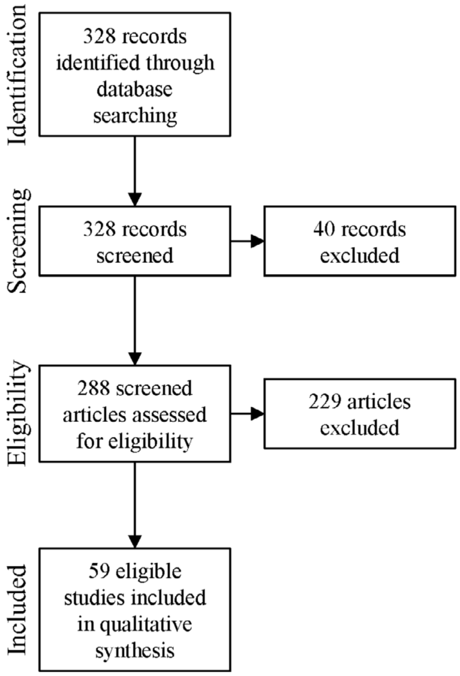

Fig. 1. Article selection diagram adapted from the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Moher et al. 2009).

Review framework

Forest types and locations were assigned based on study area descriptions and coordinates. Because authors utilized a variety of classification schemes, North American forest types were standardized to a classification scheme adapted from Barbour and Billings (2000). Based on dominant tree taxa and geographic locations, reviewed North American forest types included Boreal (B), Coastal Plain (CP), Eastern Deciduous (ED), Pacific Coastal–Cascadian (PCC), Piedmont (P), Rocky Mountain (RM), Subtropical (ST), and Tropical (T). Forest type descriptions outside North America were indicated as intercontinental (IC). Although not displayed in the review framework, pre-disturbance forest ages and stages of development were also recorded. However, of the 59 articles reviewed, only 25 specified age and 25 described developmental stage. Moreover, developmental stages were most commonly reported as mature, old growth, or second growth. With the exception of Sass et al. (2018) who described stem exclusion and Gill et al. (2017) who described understory reinitiation, forest disturbances were not discussed in the context of stand development models (e.g., Oliver and Larson 1996, Franklin et al. 2002).

To indicate inter-disturbance recovery time, the years disturbance events occurred were listed in the review framework. Most disturbances fit one of seven disturbance-type categories: bark beetles, drought, fire, moths, wind, salvage logging, or intensive forest management. Bark beetles included *Dendroctonus brevicomis* (Stevens-Rumann et al. 2015), *D. ponderosae* (Harvey et al.

2014a, b, Agne et al. 2016), *D. pseudotsugae* (Harvey et al. 2013, Stevens-Rumann et al. 2015), and *D. rufipennis* (Kulakowski et al. 2013, Carlson et al. 2017). Droughts consisted of discrete periods of exceptionally dry conditions, triggered by anomalously high temperatures and low moisture availability (Peters et al. 2011, Keith et al. 2012). Fire included prescribed fires and wildfires. Moths consisted of a *Lymantria monacha* outbreak (Bottero et al. 2013), and successive *Epirrita autumnata* and *Operophtera brumata* outbreaks (Karlsen et al. 2013). Wind events included blowdown (Buma and Wessman 2011, D'Amato et al. 2011), downbursts (Peterson and Leach 2008a, Lang et al. 2009), hurricanes (Robertson and Platt 2001, Teh et al. 2009, Bonilla-Moheno 2012, Sass et al. 2018), tornadoes (Gagnon and Platt 2008, White et al. 2014, Kleinman et al. 2017, Oldfield and Peterson 2019), and a catastrophic storm (Bottero et al. 2013). Salvage logging was conducted after wind and before fire, after wind without subsequent fire, and after fire. Intensive forest management (IFM; sensu Stokely et al. 2018) was used to describe clear-cut harvesting, experimental manipulation, and other related silvicultural entries (e.g., replanting and herbicide application). A psyllid insect (*Cardiaspina* spp.) outbreak was also described (Keith et al. 2012).

Response variables related to forest recovery were recorded to determine how impacts of compound interactions were described and to identify which forest recovery metrics were most often utilized. This process also contributed to an outcome-level assessment in which study results were assessed in relation to the type of supporting data collected (Moher et al. 2009). Forest recovery response variables were restricted to those that measured forest resilience (i.e., recovery time or trajectory), not resistance (i.e., disturbance probability, extent, intensity, or severity). For instance, post-disturbance plant establishment (e.g., seedling composition and density) was considered a metric of forest recovery, but disturbance-mediated plant mortality, which is a metric of disturbance severity, was not (Keeley 2009). In the review framework, the "+" sign indicated amplifying compound interactions in which one disturbance enhanced the impact of another disturbance by reducing forest resilience. Alternatively, the "−" sign indicated buffering compound interactions in which one disturbance reduced the impact of another disturbance by increasing forest resilience (Cannon et al. 2017). Disturbances that did not interact to impact resilience were marked "0."

RESULTS AND DISCUSSION

Wind and fire

Investigations of compound forest disturbances have escalated over the past two decades (Fig. 2). Wind disturbance and fire composed the most well-documented disturbance combination reviewed (Table 1). Consistent with the other disturbance combinations reviewed, the most

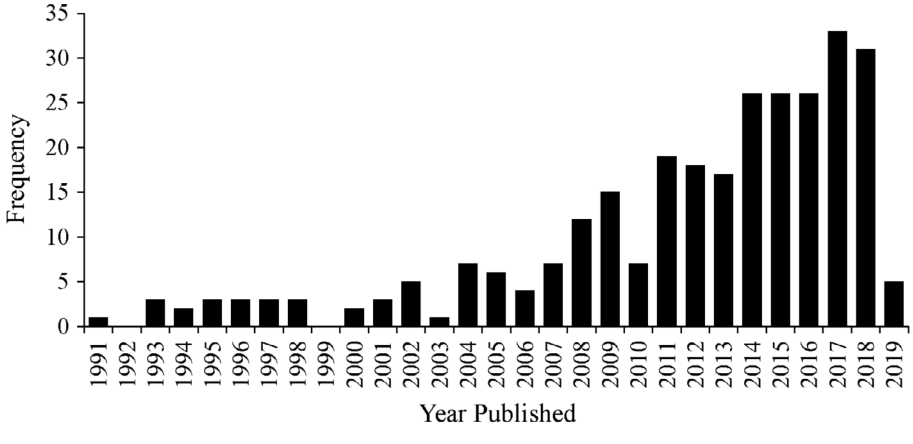

Fig. 2. Frequency of the 288 screened articles that referred to multiple forest disturbances displayed by year of publication. Year 2019 is incomplete because database searching ended in April 2019.

Table 1. Articles reviewed in this study sorted by the most common disturbance combinations, types of compound interactions (buffering −, amplifying +, neutral 0), and time between disturbance events.

Combination (disturbance 1 and disturbance 2)	Compound interaction	Forest type and location	Disturbance 1 dates	Disturbance 2 dates	Reference	Scenario
Wind and fire	−/+	P—Georgia, USA	2012	2013	Cannon et al. (2019)	
	+	CP—South Carolina, USA	1989	1990	Smith et al. (2011)	
	+	CP—Louisiana, USA	2000	2004	Gagnon and Platt (2008)	
	+	RM—Colorado, USA	1997	2002	Buma and Wessman (2011)	I
	+	RM—Colorado, USA	1997	2002	Buma and Wessman (2012)	I
	+	RM—Colorado, USA	1997	2002	Buma et al. (2014)	I
	+	RM—Colorado, USA	1997	2002	Gill et al. (2017)	
	+	RM—Colorado, USA	1997	2002	Kulakowski et al. (2017)	I
	+	B—Minnesota, USA	1999	2007	Bradford et al. (2012)	I
	+	B—Minnesota, USA	1999	2007	D'Amato et al. (2011)	I
	0	B—Minnesota, USA	1999	2007	Mitchell et al. (2016)	I
Post-wind salvage logging and fire	−	RM—Colorado, USA	1999–2001	2002	Buma and Wessman (2011)	II
	−	RM—Colorado, USA	1999–2001	2002	Buma and Wessman (2012)	II
	+	RM—Colorado, USA	1999–2001	2002	Buma et al. (2014)	II
	+	B—Minnesota, USA	1999–2002	2007	Bradford et al. (2012)	II
	+	B—Minnesota, USA	1999–2002	2007	D'Amato et al. (2011)	II
	+	B—Minnesota, USA	1999–2002	2007	Mitchell et al. (2016)	II
Repeat fires	+	IC—Victoria, Australia	2003 and/or 2007	2007 and/or 2013	Fairman et al. (2017)	
	+	IC—León, Spain	1998	2012	Taboada et al. (2013)	I
	+	PCC—Oregon, USA	1987	2002	Donato et al. (2016)	
	+	IC—Victoria, Australia	1939	1983 and/or 2009	Bowd et al. (2018)	I
	+	IC—Victoria, Australia	1939	1983 and/or 2009	Bowd et al. (2019)	I
	0	IC—Catalonia, Spain	1994	1998	Bonfil et al. (2014)	
	0	RM—New Mexico, USA	1977, 1996, and/or 2000	2011	Haire et al. (2017)	
	0	PCC—California, USA	2000	2012	Nemens et al. (2009)	
	0	PCC—Oregon, USA	1987	2002	Donato et al. (2009)	
Bark beetle outbreaks and fire	+	RM—Colorado, USA	2004–2013	2013	Carlson et al. (2017)	
	+	RM—Wyoming, USA	1995–2004	2008	Harvey et al. (2013)	
	0	RM—Wyoming, USA	2006–2008	2008	Harvey et al. (2014a)	I
	0	RM—Idaho, USA	2009–2011	2011	Harvey et al. (2014b)	I
	0	RM—Wyoming, USA	2003–2009	2011	Harvey et al. (2014a)	II
	0	RM—Montana, USA	2001–2008	2011	Harvey et al. (2014b)	II
	0	RM—Idaho and Montana, USA	1999–2004	2007	Stevens-Rumann et al. (2007)	
	0	PCC—Oregon, USA	1997–2004	2012	Agne et al. (2016)	
	0	RM —Colorado, USA	1940–1949	2002	Kulakowski et al. (2017)	II

(Table 1. Continued.)

Combination (disturbance 1 and disturbance 2)	Compound interaction	Forest type and location	Disturbance 1 dates	Disturbance 2 dates	Reference	Scenario
Fire and salvage logging	+	B —Alberta, Canada	2001	2001–2002	Cobb et al. (2007)	I
	+	B—Alberta, Canada	2001	2001–2002	Kishchuk et al. (2007)	
	+	IC—Victoria, Australia	1939 and 2009	2009–2010	Bowd et al. (2018)	II
	+	IC—Victoria, Australia	1939 and 2009	2009–2010	Bowd et al. (2019)	II
	+	PCC—California, USA	2002	2003	Knapp and Ritchie (2018)	
	+	IC—Canary Islands, Spain	2008	2009	Hernández-Hernández et al. (2017)	
	+	IC—León, Spain	1998 and 2012	1999	Taboada et al. (2013)	II
	+	IC—León, Spain	1998 and 2012	1999 and 2014	Taboada et al. (2013)	III
	0	IC—León, Spain	2012	2013 or 2014	Taboada et al. (2013)	IV
Wind and salvage logging	+	CP—Alabama, USA	2011	2011	Kleinman et al. (2015)	
	+	ED—Alabama, USA	2011	2011	White et al. (1989)	
	+	ED—Wisconsin, USA	1977	1978–1979	Lang et al. (2013)	
	+	ED—New Hampshire, USA	1938	ca. 1938–1943	Sass et al. (2016)	I
	+	CP—Tennessee, USA	1999	ca. 1999–2002	Peterson and Leach (2011)	
	+	ED—Georgia, USA	2011	2012–2013	Oldfield and Peterson (2014)	
	+	IC—Aosta Valley, Italy	1990	1992–1993	Bottero et al. (2013)	I
Repeat IFM	−/+	IC—Catalonia, Spain	1992	2002	López et al. (2009)	
	+	RM—British Columbia, Canada	1993–1994	1993–1994	Kranabetter et al. (2016)	
	+	PCC—Washington, USA	1999–2000	2000	Peter and Harrington (1998)	
	+	PCC—British Columbia, Canada	2002	2002–2003	Starzomski and Srivastava (2018)	
	+	CP—Florida, USA	2007	2008 and 2010	Ober and DeGroote (2018)	
	+	IC—Guangxi Zhuang Autonomous Region, China	1991	1998	Wen et al. (1990)	
	+	IC—Jämtland County, Sweden	1985	1996–1998	Strengbom and Nordin (2018)	
IFM and fire	+	CP—Georgia, USA	1998–1999	1998–2003	Kirkman et al. (2012)	
	+	ED—Alabama, USA	2005 or 2006	2006 or 2007	Sutton et al. (2012)	
	+	CP—Mississippi, USA	1999	2000, 2003, and 2006	Iglay et al. (2014)	
	+	B—Ontario, Canada			Pidgen and Mallik (2008b)	
	+	B – Alberta, Canada	1999	2001	Cobb et al. (2007)	II
	+	CP—Louisiana, USA	1984–1985	1987 and 2000	Coleman et al. (2008)	
	+	B—British Columbia, Canada	1997–2004	2010	Ton and Krawchuk (2009)	

(Table 1. Continued.)

Combination (disturbance 1 and disturbance 2)	Compound interaction	Forest type and location	Disturbance 1 dates	Disturbance 2 dates	Reference	Scenario
Fire and IFM	+	IC—KwaZulu-Natal, South Africa	2005	2005–2006	Schutz et al. (2018)	
	+	IC—Catalonia, Spain	1994 and/or 1998	1999	Bonfil et al. (2014)	II
	+	IC—Victoria, Australia	1939 and 1983	2009–2010	Bowd et al. (2018)	III
	+	IC—Victoria, Australia	1939 and 1983	2009–2010	Bowd et al. (2019)	III
	+	IC—Victoria, Australia	1939	1980–1985 or 2009–2010	Bowd et al. (2018)	IV
	+	IC—Victoria, Australia	1939	1980–1985 or 2009–2010	Bowd et al. (2019)	IV
IFM and wind	+	ST—Río Grande, Puerto Rico	1989	1989 and 1998	Teh et al. (2018)	
	+	ED—New Hampshire, USA	1929	1938	Sass et al. (2016)	II
Drought and psyllid insect outbreak	+	IC—New South Wales, Australia	2002–2003	2002–2003	Keith et al. (2009)	
Drought and fire	−/+	B—Moscow, Idaho			Sparks et al. (2018)	
Repeat drought	+	IC—Western Australia, Australia	2006–2007	2010–2011	Matusick et al. (2009)	
IFM and drought	+	T—Oaxaca, Mexico	1990	1997–1998	Valdés et al. (2016)	
Fire and wind	+	ST—Florida, USA	1989	1992	Robertson and Platt (2013)	
Repeat wind	+	T—Quintana Roo, Mexico	2005	2005	Bonilla-Moheno (2012)	
Repeat moth outbreaks	+	IC—Finmark County, Norway	2002–2004	2005–2006	Karlsen et al. (2017)	
Moth outbreak and salvage logging	+	IC—Aosta Valley, Italy	1984–1990	1991–1992	Bottero et al. (2013)	II

Notes: Intensive forest management (IFM) was used to describe experimental manipulation, logging, and other silvicultural entries. North American forest types included Boreal (B), Coastal Plain (CP), Eastern Deciduous (ED), Pacific Coastal–Cascadian (PCC), Piedmont (P), Rocky Mountain (RM), Subtropical (ST), and Tropical (T). Studies located outside of North America are indicated as intercontinental (IC). Articles that described multiple disturbance combinations are distinguished by scenario numbers.

common forest recovery response variables involved woody plants, but a range of other variables were also measured (Fig. 3). Also consistent with the broader literature, the occurrence and direction of compound wind-and-fire interactions sometimes depended on which response variables were considered. This concept was exemplified by an experimental wind-and-fire study in which rapid *Rhus copallinum* recruitment indicated an amplifying interaction, but increased biomass of sapling regrowth indicated a buffering interaction (Cannon et al. 2019). Enhanced *R. copallinum* establishment paralleled other compound interactions where clonal regrowth of sprouting plants was observed. Indeed, based on clonal *Arundinaria gigantea* densities, Gagnon and Platt (2008) reported that wind and fire could result in dense, monotypic bamboo stands.

Outside of the southeastern United States, two other well-studied wind-and-fire combinations occurred in the Minnesota subboreal and Colorado Rocky Mountains (Fig. 4). In both locations, clonal *Populus tremuloides* sprouted prolifically. However, a range of other forest responses were observed. In Minnesota, although postfire seedling densities indicated a potential transition to a *P. tremuloides*-dominated state, multivariate analyses did not indicate compositional differences in

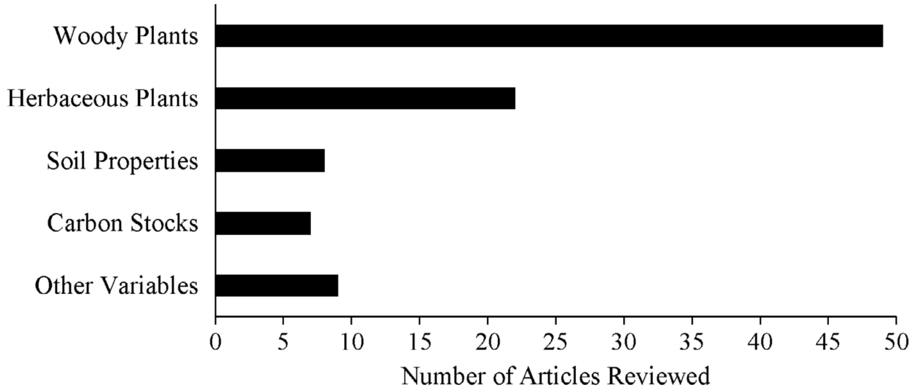

Fig. 3. Response variables used to assess forest recovery displayed by the frequency of reviewed articles that utilized them. Soil properties included microtopographic variability and forest floor litter, fibric, and humic horizons. Other variables included arthropods, bryophytes, fungi, and herpetofauna.

shrub and tree regeneration (D'Amato et al. 2011). Net forest carbon loss was attributed to wind-induced increases in deadwood and forest floor carbon pools, which were subsequently consumed by fire (Bradford et al. 2012). Nonetheless, despite increased fire severity on wind-and-fire impacted sites (Fraver et al. 2011), forest floor and soil mercury levels were comparable to fire-only sites (Mitchell et al. 2012).

In Colorado, altered canopy succession and carbon stock recovery also signaled amplifying compound interactions. Wind-induced fuel loading was linked with larger burned patches, greater fire temperature and duration, and increased *Pinus contorta* cone consumption (Buma and Wessman 2011). Because of cone consumption and greater dispersal requirements, a paucity of postfire *P. contorta* seedlings was observed, which indicated a potential transition to a *P. tremuloides*-dominated state (Buma and Wessman 2012, Kulakowski et al. 2013). Wind-and-fire impacted sites also exhibited greater successional instability over a 13-yr period compared with unburned wind-disturbed sites (Gill et al. 2017). Regarding black carbon (i.e., decay-resistant charcoal), Buma et al. (2014) predicted a net loss over the fire-return interval on wind-and-fire impacted sites, where black carbon formation was likely offset by consumption.

Post-wind salvage logging and fire

Some wind-and-fire investigations also examined the impacts of salvage logging between wind and fire. Compound interactions were documented in all instances; however, in the Colorado combination, response variable selection determined whether interactions were amplifying or buffering. Regarding postfire tree regeneration, a buffering compound interaction was observed. By reducing fuel loading, salvage logging reduced fire intensity and *P. contorta* cone consumption (Buma and Wessman 2011). As such, postfire *P. contorta* regeneration was greater on salvaged sites, exemplifying increased forest resilience (Buma and Wessman 2012). Regarding black carbon, however, the compound interaction was amplifying, with the greatest net losses expected on salvaged sites where a considerable amount of carbon was extracted (Buma et al. 2014).

In Minnesota, post-wind salvage logging and fire exhibited all amplifying compound interactions. By removing deadwood, salvage logging homogenized postfire plant communities and was expected to have lasting impacts on forest recovery (D'Amato et al. 2011). Reduced downed woody debris and standing snag carbon pools also indicated potential for altered or delayed forest carbon recovery (Bradford et al. 2012). Moreover, drier conditions, exposed mineral soil, and potentially compacted litter on salvaged sites increased forest floor susceptibility to mercury emission and volatilization (Mitchell et al. 2012).

Repeat fires

Forest resilience to successive wildfires was indicated by persistence of remotely sensed

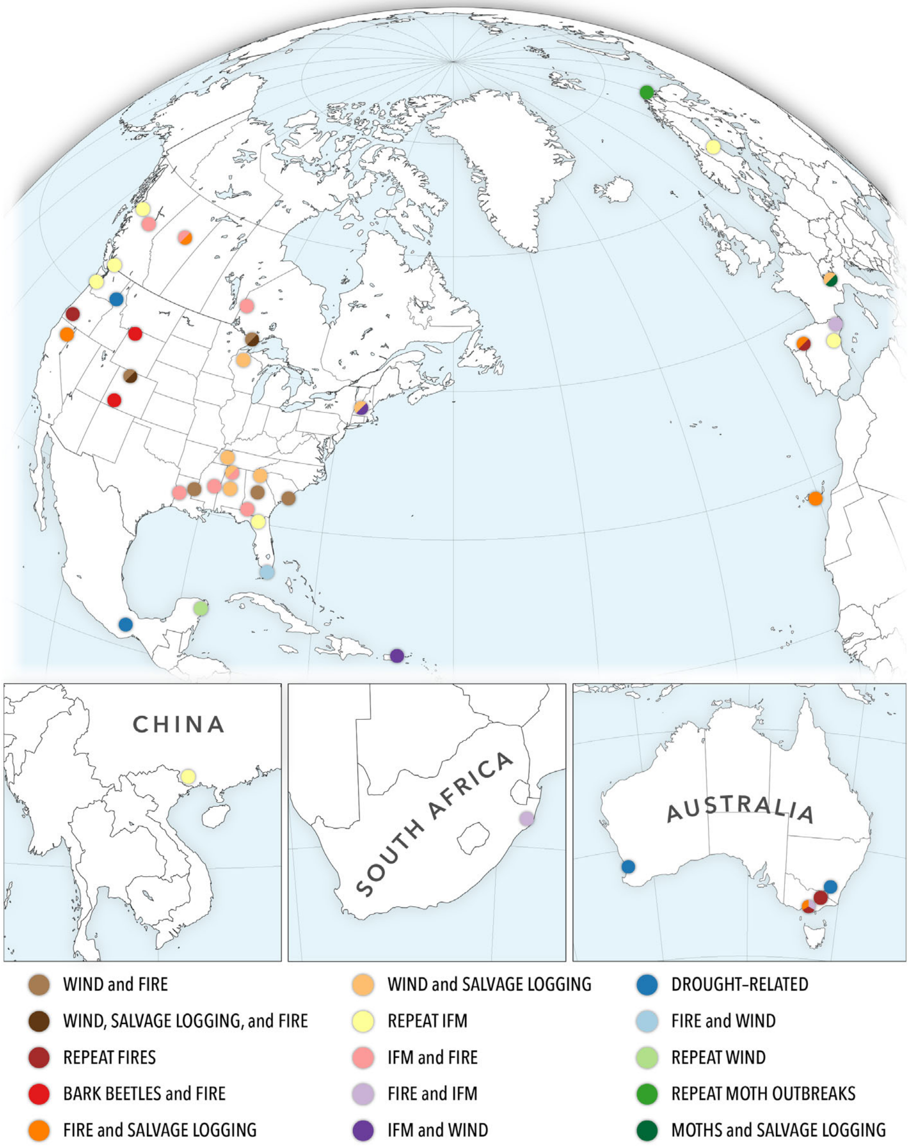

Fig. 4. Geographic distribution of the compound forest disturbances reviewed. Study location (circle) colors correspond to disturbance combination descriptions. Divided circles indicate study locations where multiple types of compound disturbance combinations occurred. Intensive forest management (IFM) includes experimental manipulation, logging, and other silvicultural entries.

refugial plant communities (Haire et al. 2017), persistence of core plant species (Donato et al. 2009), and the sustained ability of sprouting plants to recharge underground carbon stocks and regrow after fire (Bonfil et al. 2004, Nemens et al. 2018). By contrast, Fairman et al. (2017) attributed reduced *Eucalyptus pauciflora* resprouting ability to a reduction in viable growth buds and increased vulnerability of immature stems to recurring fire. Sites subject to multiple fires also exhibited potential to transition from shrub- to grass-dominated understories and develop toward more open woodland- or savanna-like structures. Taboada et al. (2018)

documented a species-specific response in which resprouting shrubs persisted after successive fires, but *Pinus pinaster*, which reproduces from serotinous cones, had insufficient time to replenish the canopy seed bank between fires. Bowd et al. (2018) also documented an increased abundance of resprouting plants and reduced populations of on-site seeders after multiple fires. Although Donato et al. (2009) documented unique plant assemblages in twice-burned sites, differences reflected additional species, not losses. Nonetheless, deadwood biomass was substantially reduced in twice-burned sites, and a deadwood biomass discrepancy was predicted to last for over 100 yr of stand development (Donato et al. 2016). Bowd et al. (2019) also documented long-lasting impacts, in which altered soil properties endured over 80 yr after a single fire, and multiple fires had amplifying effects.

Bark beetles and fire

In this review, only two beetle-and-fire investigations reported compound interactions (Harvey et al. 2013, Carlson et al. 2017). Forest resilience was attributed to ample inter-disturbance recovery time and species-specific recovery strategies. Agne et al. (2016) discussed how 8–15 yr between disturbances was likely long enough for advanced regeneration to reach larger size classes. Kulakowski et al. (2013) documented comparable postfire tree regeneration on sites unaffected or impacted by bark beetles over 50 yr prior. Whereas *Pseudotsuga menziesii* failed to provide viable seed for postfire regeneration (Harvey et al. 2013), serotinous *P. contorta* cones persisted on beetle-killed trees and contributed to postfire seedling establishment (Harvey et al. 2014a, b). Another reason proposed for undetected interactions was that high severity fires had similar impacts regardless of prefire beetle outbreaks (Stevens-Rumann et al. 2015). Indeed, Harvey et al. (2013), who documented a compound interaction, only observed this interaction in areas burned by light surface fires. Tree regeneration was low regardless of beetle outbreaks where fires were more severe. Compared with the tree regeneration-focused articles, Carlson et al. (2017) used a more generalized, Landsat-based approach to detect negative relationships between prefire beetle outbreak severity and understory vegetation recovery.

Fire and salvage logging

A unique suite of response variables was used to detect compound fire-and-salvage logging interactions. Deadwood extraction yielded suitable conditions for early-successional species associated with open habitats, thereby delaying bryophyte recovery (Hernández-Hernández et al. 2017) and reducing the compositional variability of ground beetles (Cobb et al. 2007). Kishchuk et al. (2015) attributed delayed recovery of carbon and soil organic matter to removal of charred material that would have otherwise been incorporated in forest floor recovery. However, foliar nutrition and regeneration growth converged, reinforcing that the detection of compound interactions can depend on the response variables assessed. Similarly, Knapp and Ritchie (2016) attributed reduced shrub cover and richness to mechanical impacts of salvage logging, but noted that, of the multiple functional groups and life-history categories assessed, only shrubs were significantly impacted. Bowd et al. (2018) reported that, although on-site seeders persisted in salvaged sites, resprouting species exhibited significant reductions. Soil nutrient levels and ecologically important exchangeable cations were reduced as well (Bowd et al. 2019). Disturbance frequency also influenced whether fire-and-salvage logging exhibited interactions. Taboada et al. (2018) reported that, after a single fire, salvage logging did not impact forest recovery, but with two fires, reduced seedling establishment was amplified by salvage logging.

Wind and salvage logging

The detection of compound wind-and-salvage logging interactions without subsequent fire depended on which response variables were assessed and which aspects of forest resilience were considered. For instance, Sass et al. (2018) observed parallel successional trajectories in unlogged and logged wind-disturbed sites, but noted persistent salvage-mediated structural differences, including reduced microtopographic variability. Similarly, Peterson and Leach (2008b) noted that salvage logging altered microsite conditions, but not herbaceous plant assemblages. In a companion study, salvage logging compacted soil, but did not alter the percentage of soil surface disrupted (Peterson and Leach 2008a). Furthermore, variation in woody plant diversity and compositional dissimilarity was mostly driven by wind severity, not salvage logging.

In a *Pinus palustris* woodland, salvage-mediated habitat homogenization was associated with reduced ground flora diversity and macrofungal richness and fruiting abundance (Ford et al. 2018, Kleinman and Hart 2018). However, salvaged sites hosted the greatest *P. palustris* sapling densities, indicating that recovery toward pre-disturbance canopy conditions was not delayed (Kleinman et al. 2017). In contrast, Bottero et al. (2013) attributed reduced *Picea abies* seedling establishment to the removal and piling of logs that may have otherwise served as germination sites (i.e., nurse logs). Oldfield and Peterson (2019) also documented delayed succession on salvaged sites, which, compared with unlogged sites, hosted more mid-successional species and fewer late-successional species. Nonetheless, sapling and tree density and diversity were unaffected.

The distinction between recovery time and trajectory also influenced the detection of compound interactions. White et al. (2014) predicted that sites differentially impacted by wind and logging would transition from *Quercus* to *Acer* dominance. Yet, despite similar successional trajectories, salvage logging accelerated this transition by damaging *Quercus* saplings. In contrast, Lang et al. (2009) noted that, after 25 yr, areas differentially disturbed by wind and salvage logging converged by most metrics of plant recovery, but exhibited different recovery trajectories. Salvaged sites recovered from residual stump sprouts and roots suckers instead of the seedlings, saplings, and trees that persisted in unlogged areas. Moreover, salvage logging was associated with persistent soil compaction and homogenization, reduced microtopographic variability, and increased representation of disturbance-adapted plants (Lang et al. 2009).

Repeat intensive forest management

Experimental, rather than observational, approaches can limit possible autocorrelation and pseudoreplication involved with natural experiments and are well-suited to test forest responses to multiple levels of disturbance severity (Foster et al. 2016). Strengbom and Nordin (2012) reported that experimental N enrichment had minimal impacts on vascular plant and bryophyte communities until coupled with subsequent clear-cut harvesting. Experimental approaches can also be used to examine subtle differences across treatments not possible in an uncontrolled setting. For example, Starzomski and Srivastava (2007) experimentally manipulated a moss-covered rock outcrop to demonstrate how reduced habitat connectivity lowered ecological resilience to microarthropod extraction.

A diversity of response variables can be utilized in experimental studies to detect a range of forest responses to compound disturbances. For instance, although Kranabetter et al. (2017) documented impacts of organic matter removal and soil compaction on plant and fungal community dissimilarity, beetle communities exhibited a negligible response. In plantations subject to repeated experimental raking, changes in arthropod abundance manifested differentially across arthropod orders of interest (Ober and DeGroote 2014). López et al. (2009) described a trade-off between aboveground growth and carbon stock renewal in twice-thinned stands. Whereas increased biomass and densities of resprouting individuals signaled a buffering interaction, reduced lignocarbon reserves indicated an amplifying interaction. Wen et al. (2010) surveyed understory plant communities in plantations subject to one or two rotations of continuous cropping. Compared with first rotation stands, second rotation stands hosted altered understory plant communities, characterized by reduced plant diversity and cover of woody growth forms. Peter and Harrington (2009) also documented reduced understory plant cover and diversity in clear-cut stands subject to annual herbicide application, which consequently accelerated the establishment of planted seedlings.

Intensive forest management and fire

Because prescribed fire is another form of intensive management, the combination of prescribed fire after other silvicultural entries can also be described as repeat intensive forest management. These combinations illustrated how compound disturbances can sometimes be utilized to achieve desired conditions. In particular, Kirkman et al. (2007) demonstrated how incomplete overstory removal and prescribed fire could induce desired compositional shifts in a forest plantation without sacrificing structural and functional continuity. Iglay et al. (2014) documented a trade-off between desired structure and diversity, in which herbicide and prescribed fire achieved target midstory hardwood reductions but also reduced understory plant diversity. Sutton et al. (2013) reported that sites subject to experimental thinning and prescribed burning hosted distinct herpetofaunal assemblages associated with reduced canopy cover and litter depth. Pidgen and Mallik (2013) also reported divergent recovery trajectories, in which some trees, shrubs, and other plants with vegetative regeneration strategies had insufficient time (ca. two years) to recovery between clear-cut harvesting and prescribed fire.

The combination of logging and wildfire also induced a range of forest responses. Although Coleman et al. (2008) reported that logged sites exhibited comparable postfire plant assemblages and successional trajectories to unlogged sites, subtle species-specific and structural differences were observed. In contrast, Cobb et al. (2007) documented conspicuous differences in beetle assemblages, characterized by reduced compositional variability, and Ton and Krawchuk (2016) documented distinct differences in plant assemblages, characterized by increased representation of disturbance-adapted species. Altered recovery trajectories were also indicated by a reduction in postfire *P. contorta* seedling densities, attributed to clear-cut-mediated seed source reductions (Ton and Krawchuk 2016).

Fire and intensive forest management

Mechanical impacts of clear-cut logging in fire-regenerated stands induced comparable effects to postfire salvage logging. Key soil metrics including organic carbon and available phosphorus and potassium were reduced (Bowd et al. 2019), in addition to a reduction in resprouting plants (Bowd et al. 2018). Resprouting plants also exhibited a range of response variable-specific responses to experimental postfire defoliation. For example, although leaf biomass allocation increased in resprouting *Acacia karroo* saplings, root carbohydrate reserves, shoot diameter, and stem biomass were reduced (Schutz et al. 2011). Bonfil et al. (2004) reported that, although *Quercus cerrioides* was resilient to fire and low-intensity manipulation (i.e., clipping), *Q. ilex* was not. Nonetheless, the number and growth of both *Q. cerrioides* and *Q. ilex* were reduced by high-intensity postfire manipulation (i.e., cutting or concentrated burning with a propane torch).

Intensive forest management and wind

The literature on forest responses to logging and subsequent wind disturbance is expansive and unresolved (Albrecht et al. 2012, Coates et al. 2018). However, we reviewed only two articles that assessed logging followed by wind disturbance, indicating the inherent limitations of our restricted inclusion criteria. Consistent with the other articles reviewed, the detection of compound forest clearing and wind disturbance interactions was contingent on the response variables considered. Like post-hurricane salvage logging, sites clear-cut prior to a hurricane followed comparable successional trajectories to unlogged sites, but exhibited persistent structural differences (Sass et al. 2018). Teh et al. (2009) reported that, whereas soil carbon and nutrient pools were resilient to experimental gap formation and multiple hurricanes, post-hurricane fine-root production was reduced in cleared sites.

Drought

Response variable selection also influenced the detection and direction of drought-related interactions. Sparks et al. (2018) documented a buffering interaction in which severely water-stressed saplings exhibited enhanced postfire recovery, indicated by increased rates of bud production. However, postfire height and diameter growth decreased with increasing drought severity, indicating an amplifying interaction. Valdés et al. (2006) noted that, although drought reduced total fine-root and ectomycorrhizal-root biomass after seed tree harvesting and prescribed fire, soil inoculum potential remained relatively stable. Another response variable-specific interaction was documented by Matusick et al. (2016), in which successive droughts induced a structural transformation, but the relative abundance of dominant tree species remained stable. Keith et al. (2012) also examined forests subject to successive droughts, but the compound interaction of interest involved the combined impacts of insect attack and drought. Whereas forests undergoing drought alone still served as carbon sinks, simultaneous drought and insect stress resulted in net carbon losses (Keith et al. 2012).

Other combinations

In addition to the drought-related combinations, four disturbance combinations were unique to individual studies in the review framework. Robertson and Platt (2001) monitored epiphytic bromeliads in subtropical hammocks differentially impacted by pre-hurricane lightning fire. Because burned bark and branches provided less stable substrates, the hurricane disproportionately dislodged epiphytes in burned sites, thereby delaying recovery toward pre-disturbance epiphytic distributions. Although resprouting conferred structural resilience to two hurricanes in quick succession, compositional shifts in the relative abundance of more and less resistant species were observed (Bonilla-Moheno 2012). Karlsen et al. (2013) described consecutive moth outbreaks that induced understory shrub-to-grassland transitions. However, transitions only occurred in nutrient-limited sites, as nutrient-rich sites hosted a higher diversity of understory plants that contributed to forest resilience. Like post-wind salvage logging, Bottero et al. (2013) attributed reduced *P. abies* seedling establishment after a moth outbreak and salvage logging to the removal and piling of logs that may have otherwise served as germination sites.

SYNTHESIS

Forest responses to compound disturbances range from accelerated or delayed recovery toward pre-disturbance conditions to succession and development toward alternative states. Although compound interactions were detected in most articles reviewed, an outcome reporting bias likely increased the chances of detecting articles that reported significant interactions (Moher et al. 2009). For instance, all of the wind-and-salvage logging combinations exhibited compound interactions, but post-wind salvage logging can be conducted in ways that maintain forest resilience (Royo et al. 2016). Consistent with a recent review of wind-and-fire interactions (Cannon et al. 2017), a paucity of buffering interactions that increased forest resilience was identified. Moreover, the detection of buffering interactions was contingent on which response variables were assessed. All disturbance combinations that exhibited buffering compound interactions also exhibited amplifying interactions that reduced forest resilience in some capacity. For example, although post-wind salvage logging enhanced *P. contorta* recovery (buffering interaction; Buma and Wessman 2011, 2012), it also amplified black carbon stock reductions (amplifying interaction; Buma et al. 2014). Whereas experimental wind and fire enhanced sapling regrowth (buffering interaction), *R. copallinum* recruitment increased disproportionately (amplifying interaction; Cannon et al. 2019). We contend more research on buffering interactions is needed to improve understanding of compound disturbances and encourage researchers to examine a broader range of response variables to achieve a more complete understanding of compound interactions.

Indeed, the response variables used to assess forest recovery often determined whether a compound interaction was detected. These distinctions most commonly involved differential recovery related to the expression of species-specific life-history strategies (Buma and Wessman 2012, Knapp and Ritchie 2016, Bowd et al. 2018), but also involved a distinction between recovery time and trajectory (Lang et al. 2009, White et al. 2014) and forest succession and development (Bonilla-Moheno 2012, Matusick et al. 2016, Sass et al. 2018). Other disturbance combinations only exhibited compound interactions at specific forest strata (Bradford et al. 2012, Mitchell et al. 2012) or scales, such as changes in individual species but not overall communities (Coleman et al. 2008). We hope some of the less commonly reported metrics, such as bryophyte, beetle, and/or fungal assemblages, inspire future studies to conduct more comprehensive investigations of forest ecosystem recovery.

Compound disturbance interactions were recorded in only six countries outside of North America, indicating the need for more research on this topic outside of North America. Within North America, however, investigations were well-distributed, indicating that no particular region or forest type has disproportionately influenced our conceptual understanding of compound disturbances. Regarding disturbance types, however, a disproportionate focus on fire, wind, and salvage logging indicated the need for more research to focus on other understudied disturbance types such as floods, ice storms, and landslides.

Commonly reported disturbance legacies that facilitated compound interactions included seed source reduction, deadwood accumulation and reduction, and increased light and growing space availability. For instance, reduced postfire regeneration was attributed to seed source reduction by a preceding fire (Taboada et al. 2018), bark beetle outbreak (Harvey et al. 2013), and clearcut logging operation (Ton and Krawchuk 2016). Salvage-mediated deadwood extraction resulted in reduced black carbon formation (Buma et al. 2014) and delayed carbon and soil organic matter recovery (Kishchuk et al. 2015). Deadwood extraction also homogenized plant communities (Kleinman et al. 2017), and delayed bryophyte community recovery by improving habitat suitability for early-successional assemblages associated with open habitat (Hernández-Hernández et al. 2017). Kranabetter et al. (2017) attributed increased representation of invasive plants and reduced fungal richness, in part, to organic matter removal, which increased mineral soil exposure and reduced soil moisture and soil porosity. Cobb et al. (2007) attributed reduced compositional variability of ground beetles in logged areas, in part, to the absence of species adapted to damp microclimates beneath logs. By defoliating shrubs, moths facilitated grass proliferation in response to increased light and nutrient availability from moth excreta and elimination of allelopathic shrubs (Karlsen et al. 2013).

Inter-disturbance recovery time also influenced the occurrence of compound interactions (Pidgen and Mallik 2013, Carlson et al. 2017, Taboada et al. 2018). In particular, Bowd et al. (2018) and Taboada et al. (2018) described how on-site seeders had insufficient time to mature and reproduce between successive fires. Although compound interactions generally involved five or fewer years between successive disturbance events, and this five-year benchmark may help characterize compound disturbances, it should not be considered a defining principle. Indeed, D'Amato et al. (2011) and Bradford et al. (2012) documented compound interactions between wind and fire separated by eight years, and Harvey et al. (2014a, b) did not document compound interactions between bark beetle outbreaks and fires separated by 0–3 yr. Nonetheless, over half of the compound interactions documented involved a year or less between disturbance events.

Based on our systematic review, we make the following observations and recommendations:

1. Progress in compound disturbance ecology has been largely influenced by disturbance combinations involving fire, wind, and salvage logging. A disproportionate focus on these disturbance types may bias our understanding of compound interactions, and we encourage more research on other understudied disturbance types.
2. Most compound disturbances exhibited amplifying interactions that reduced forest resilience. To understand ways forest resilience is enhanced, we recommend more research focus on buffering interactions.
3. A disproportionate amount of research has been conducted in North America. To ensure understanding of compound disturbances is not biased toward the climates and life-forms of this continent, more work is needed in other understudied regions and forest types.
4. Compound disturbances were most often mediated by disturbance legacies involving reduced seed source availability, deadwood accumulation and reduction, and increased light and growing space availability.
5. To date, compound forest disturbance investigations have typically examined events separated by five or fewer years. To advance understanding of compound disturbances, we recommend more studies are developed to investigate longer inter-disturbance recovery periods.
6. Assessments of forest recovery were focused primarily on woody plant-based metrics. To achieve a more complete understanding of compound interactions, we recommend the use of a diversity of other metrics including arthropods, bryophytes, carbon stocks, fungi, herbaceous plants, herpetofauna, and soil properties, which were also encountered in this review.
7. Ultimately, efforts to quantify ecosystem resilience to interacting disturbances are

contingent on the response variables measured. Going forward, we encourage the development of a more holistic resilience framework that considers multiple response variables.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2962/full