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Synthesis

Nurturing resilient forest biodiversity: nest webs as complex adaptive systems

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ABSTRACT. Forests are complex adaptive systems in which properties at higher levels emerge from localized networks of many entities interacting at lower levels, allowing the development of multiple ecological pathways and processes. Cavity-nesters exist within networks known as "nest webs" that link trees, excavators, e.g. woodpeckers, and nonexcavators (many songbirds, ducks, raptors, and other organisms) at the community level. We use the idea of panarchy (interacting adaptive cycles at multiple spatio-temporal scales) to expand the nest web concept to levels from single tree to biome. We then assess properties of nest web systems (redundancy, heterogeneity, memory, uncertainty, and nonlinearity) using examples from our studies in temperate, subtropical, and tropical forests of the Americas. Although nest webs from Chile, Canada, Argentina, and Ecuador have independent evolutionary histories, structures, and disturbance regimes, they share the main properties of complex adaptive systems. Heterogeneity, redundancy, and memory allow nest web systems to absorb some degree of disturbance without undergoing a regime shift; that is, without changing their basic structures and functions, i.e., the system's identity. Understanding nest webs as complex adaptive systems will inform management practices to nurture the resilience of forest biodiversity in the face of local, regional, and global social-ecological changes.

Key Words: *Americas; cavity-using vertebrates; complexity; forest management; memory; panarchy; resilience; social-ecological systems*

INTRODUCTION

The search for holistic, yet scientifically sound, whole-system models in forest ecology and conservation has led to an increasing interest in complex system science (Parrott and Meyer 2012, Messier et al. 2013, Filotas et al. 2014). Historically, forest biodiversity has been assessed and managed through the lens of a single dominant objective, which can result in counterproductive conservation and management practices (Puettmann et al. 2009). For example, fire suppression policies to control the loss of green-tree forests led to unpredicted declines in the red-listed Black-backed Woodpecker (*Picoides arcticus*; Hutto 2006). Forest ecosystems are, in fact, prototypical examples of complex adaptive systems (CAS) in which properties at higher levels (Gunderson and Holling 2002, Messier and Puettmann 2011, Parrott and Meyer 2012), emerge from self-organized networks of many entities (individuals, species, guilds) interacting at lower levels (Levin 1998, Strogatz 2001, Simard et al. 2013). Gunderson and Holling (2002) proposed the concept of panarchy as a framework of rules that captures the evolutionary characteristics of adaptive cycles (Table 1), while allowing hierarchical nesting of these cycles across spatial and temporal scales. Panarchy can be used to describe how complex social-ecological systems, such as forests, are interlinked in multilevel adaptive cycles of growth (r), conservation (K), release (Ω), and reorganization (α; Table 1). This proposal by Gunderson and Holling (2002), triggered a major discussion about the role of panarchy in forest resilience, the latter defined as the capacity of forests to adaptively persist following anthropogenic and natural disturbances while retaining their essential structures and functions, i.e. system's identity (Holling 1973, Messier et al. 2013).

About 1900 species of birds (~18% of all birds) and many other vertebrates use tree cavities for nesting and roosting, constituting a key component of forest biodiversity that is traditionally managed at the stand or single-tree level (Bunnell and Dunsworth 2009, Van der Hoek et al. 2017). Cavity-users interact in networks known as "nest webs," conventionally viewed as hierarchical and commensal, with resource (cavity) flow from trees facilitated by excavators, e.g., woodpeckers, to nonexcavators, e.g., many songbirds, ducks, raptors, and other organisms (Martin and Eadie 1999, Martin et al. 2004). Excavators are considered to facilitate nonexcavators, which then compete amongst themselves for the cavity resource (Fig. 1). The simplicity of the hierarchical nest web model encouraged researchers to initiate community-level nest web studies in many forests globally, allowed us to analyze cavity-nesting communities as bi- or tri-partite ecological networks, and facilitated communication with forest managers and the public (Martin et al. 2004, Cockle and Martin 2015, Ruggera et al. 2016, Altamirano et al. 2017, Manikandan and Balasubramanian 2018).

Outside the conventional framework, nest webs experience feedback loops among guilds and interact with other networks at multiple levels, such that a whole-system view could be important for management (Floyd and Martin 2016, Ibarra et al. 2017*a*). In

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Table 1. Panarchy, adaptive cycles, and properties of nest webs as complex adaptive systems (CAS).

Term	Definition in a nest web context
Panarchy	Nest webs exhibit adaptive cycles at four interacting levels: (1) the single cavity-tree, (2) the integrated community of cavity nesters, i.e., a nest web of a single forest type, (3) the landscape mosaic of forests, i.e., nest webs that interact across forest types within a biome, and (4) the regional pattern of nest webs, i.e., mosaics of nest webs that interact across landscapes through, for example, colonization, range expansions, and other changes that are affected by broad-scale cycles. The lower level cycles are dynamic, adaptive, and sensitive to small changes with potential for creative transformations. The larger level cycles are generally slower, stable, and robust, constraining the system against the dynamism of the smaller, generally faster cycles. Continuous shuffling through these interacting loops provides the opportunity for novel assortments and configurations in the ecosystem.
Adaptive cycle	The adaptive cycle is a representation of system dynamics at a particular spatial and temporal scale. The system at that scale cycles through four sequential stages, from rapid growth (r) such as when a population, e.g., of a cavity nester, grows, to conservation (K) such as when the population reaches carrying capacity, to release (Ω) such as when the population becomes overcrowded and vulnerable to reorganization (α) such as when uncertainty can lead to novel adjustments. Each sequential stage is present at every adaptive cycle. The adaptive cycle is shaped by three attributes: (1) the inherent potential for the system to change, (2) the degree of internal control or connectedness of the system, and (3) the adaptive capacity and resilience to unexpected shocks.
Redundancy	Degree to which organisms resemble each other in their functional roles. In nest web systems, the degree to which decay organisms, tree species, cavity nesters, and forest types produce tree cavities and nest webs with similar characteristics.
Heterogeneity	Heterogeneity is expressed by the uneven nature of interacting entities and their behaviors, spatial location, structural organization, and history. In nest web systems, interacting entities (plants, fungi, animals, forests, people) are heterogenously distributed in space, contributing to spatial heterogeneity in tree-decay processes, cavity availability, and nest web diversity.
Memory	Record of historical events that continues to influence compositional, structural, and functional states of the system. Memory of a nest web includes, for example, habitat legacies: long-lived system entities such as very old trees, cavities, and forest patches, whose presence and influence extends over a long time.
Uncertainty and nonlinearity	Uncertainty is associated with nonlinear dynamics and incomplete knowledge of the system. Sources of uncertainty, e.g., crucial nonmeasured variables, reduce our ability to predict the future state of nest web systems. They also generate variability that may be amplified by feedback loops, leading to the emergence of novel relations or structures.

addition to facilitation, interactions among excavators and nonexcavators can include competition and predation (Blanc and Walters 2008*a*, Wesołowski 2017, Wiebe 2017). Cavity-nesters disperse seeds of future nest trees and spores of the wood-decay fungi that facilitate cavity formation (Lonsdale et al. 2008, Holbrook and Loiselle 2009, Jusino et al. 2016, Tella et al. 2016, Speziale et al. 2018), but some species may also reduce recruitment of cavity trees through seed predation (Renton 2001). Underground, a network of mycorrhizal fungi connects current and future cavity trees, promoting recruitment (Simard et al. 2013). Multiscale linkages between nest webs and other networks, including social-ecological networks in which decision makers and the general public interact, give rise to structural and dynamic emergent properties of a complex adaptive system (Filotas et al. 2014).

In this synthesis paper we show how complex system science can provide a holistic, unifying model for the study of nest webs globally. We first use panarchy to represent a hierarchy of adaptive cycles, then review properties of CAS (redundancy, heterogeneity, memory, uncertainty, and nonlinearity) in nest web systems (Table 1). We draw on examples from our long-term studies across a gradient from mega-diverse tropical and subtropical forests at lower latitudes to species-poor temperate systems at higher north and south latitudes in the Americas (Table 2, Fig. 2). Finally, we link the properties of nest webs to potential forest management practices. We do this by integrating forestry into a holistic framework with the goal of helping nurture the resilience of complex adaptive nest webs in the face of local, regional, and global changes.

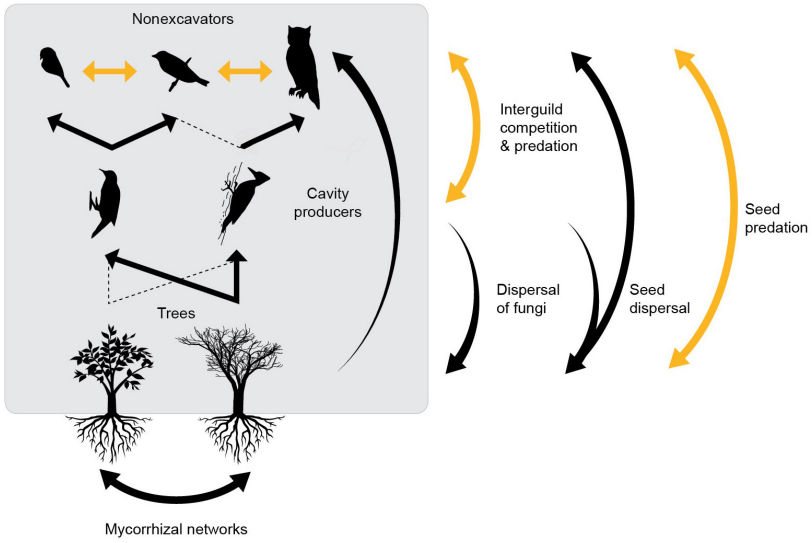
PANARCHY IN NEST WEBS

A panarchy (linked multilevel interactions) is a representation of a hierarchy of adaptive cycles (Table 1). We describe below the characteristics of each adaptive cycle in nest webs, from the smallest to the largest level (Fig. 3).

Single cavity-tree

During the growth (r) stage a seed germinates, the seedling is colonized by mycorrhizal fungi (facilitating growth and survival), and grows to a suitable size, age, and decay status for a cavity to form, for example, by excavation in a dead branch (Fig. 1; DeGraaf and Shigo 1985, Lindenmayer et al. 1993, Koch et al. 2008, Blanc and Martin 2012, Simard et al. 2013). In the conservation stage (K), micro-organisms slowly increase the size of the cavity (Edworthy and Martin 2014, Zheng et al. 2016), and it is occupied by a series of cavity-nesting vertebrates (Edworthy et al. 2017) that may also disperse seeds or fungi to and from the nest site (Simard et al. 2013, Jusino et al. 2016, Tella et al. 2016). Over time, increasing size and advancing decay might slowly increase vulnerability of the cavity to depredation and usurpation, making it less suitable for nesting vertebrates (Wesołowski and Rowiński 2004, Zhu et al. 2012, Pakkala et al. 2017). As decay advances through the cavity-tree, the system eventually reaches a state of vulnerability to stress or disturbance; for example, the cavity-bearing branch may break off, leading to a rapid release (Ω) as the tree becomes temporarily unsuitable for nesting. This may be followed by reorganization (α) that can lead to novel responses, for example, if the falling branch creates a new cavity in the tree stem, or if the tree itself falls, exiting the system, and another seedling takes its place, moving the system to a new "r" stage. These conditions are highly unpredictable and uncertain. For example, the species of seedling that replaces the old-growth tree will be influenced by the seeds and mycorrhizal propagules dispersed by prior cavity occupants. Because adaptive cycles occur simultaneously (but asynchronously) in multiple individual trees throughout a forest stand, they combine to form the adaptive cycle at the adjacent higher level (nest web community, below).

Fig. 1. A simple conventional model of nest web (grey box) with positive (black) and negative (yellow) interactions among species (Martin and Eadie 1999). Cavities flow (straight black arrows) from trees to cavity producers, i.e., excavators or decay, to nonexcavators, which compete amongst themselves for the limited cavity resource (straight yellow arrows). Weaker links are shown with broken lines. Arrows outside the grey box highlight several important feedback loops beyond the conventional nest web model.



At the transition from the conservation stage (K) to release (Ω) and the transition from reorganization (α) to growth (r), the adaptive cycle can be transformed, affecting the adaptive cycle at the adjacent higher level. For example, cutting a large tree for timber (a common practice at our study of social-ecological systems in South America) will not only stop the cycles of cavity production in that tree, but will also impact seed dispersal- and mycorrhizal networks at the community level (next adaptive cycle).

Community of cavity nesters

At the community level, we propose that the growth (r) stage is characterized by initial recruitment of short-lived, mostly excavated cavities in fast-growing pioneer tree species in early successional forest (Cockle et al. 2017). Initially, most cavities are small, low, and similar to one another, and are used by a limited set of small-bodied, disturbance-tolerant, cavity-nesting animals (Dantas Oliveira 2015). The conservation stage (K) is reached as the forest gets older and begins to include shade-tolerant tree species with longer lasting cavities, as well as large dead trees, such that a wider range of cavity types and sizes can support a diverse nest web of excavators and nonexcavators (Cockle et al. 2019*a*). At this stage, the nest web may be exposed to rapid release (Ω) because the forest is increasing in structural complexity due to individual tree mortality (from insects, disease, fire, drought, etc.) and gap-phase dynamics (Franklin and Van Pelt 2004, Zenner 2004, Caviedes and Ibarra 2017). As the forest transitions to old-growth structures during the reorganization (α) stage, the nest web will comprise a diverse suite of tree and vertebrate species, including old-growth specialists that require large decay-formed cavities in living trees, as well as large cavity-nesting seed-

Fig. 2. Species numbers of birds (grey bar), cavity-nesting birds (brown bar), and trees (green bar) in our study sites across the Americas. These sites represent a gradient of forests from relatively species-poor temperate systems at higher latitudes to species-rich subtropical and tropical forest areas at lower latitudes (closer to the equator). The distribution of forested areas in the continent is shown in green.

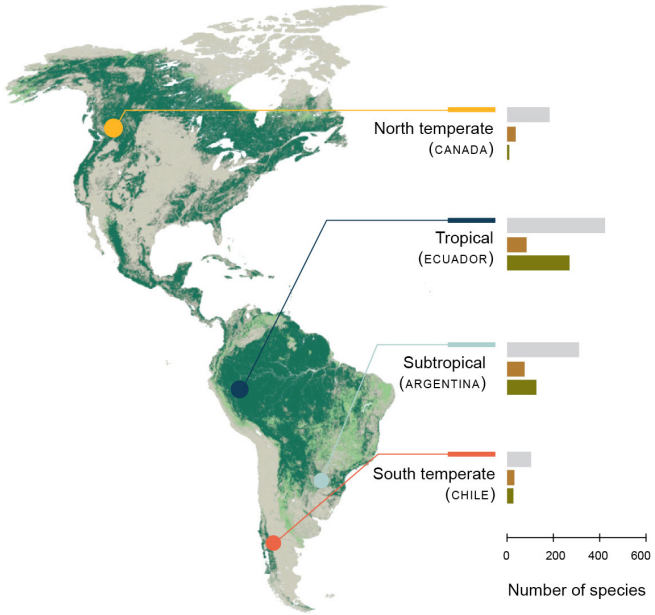
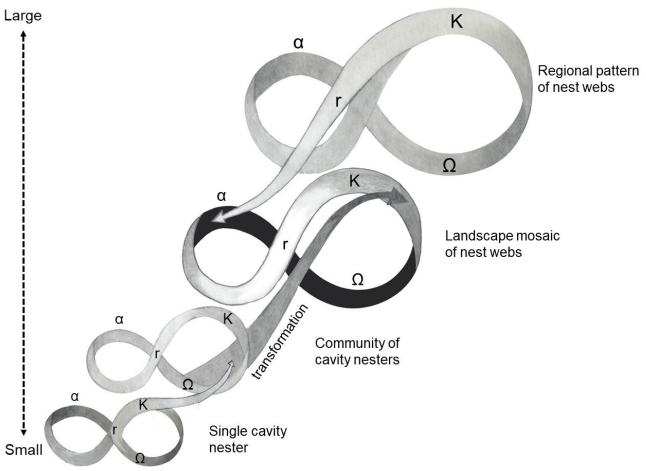


Table 2. General attributes of forest ecosystems presented in this paper.

Forest ecosystem	North temperate forest (Canada)[1]	Tropical forest (Ecuador)[2]	Subtropical forest (Argentina)[3]	South temperate forest (Chile)[4]
Geographic location (coordinates)	52°08′N, 122°08′W	0°59′S, 77°48′W	26°38′S, 54°07′W	39°16′S, 71°48′W
Elevation (m asl)	800–920	300–1200	520–700	220–1400
Forest type	Interior Douglas-fir forest	Amazonian tropical lowland and Piedmont rainforest	Atlantic forest	Andean temperate rainforest
Major recent disturbances	Wildfire, insect outbreak, clear-cut and partial cut logging, followed by planting of native trees	Forest clearing for agriculture/ livestock, clear-cut and partial cut logging, defaunation through overharvesting	Forest clearing for agriculture/ livestock/exotic tree plantations, highgrade logging, defaunation through overharvesting	Wildfire, volcanic eruption, forest clearing for agriculture/ livestock, exotic tree plantations
Current social-ecological context	Forests embedded in mosaic of small lakes, and native grasslands, maintained by low intensity fires and cattle grazing. Commercial and private land use for forestry, agriculture, recreational hunting, and fishing. Primarily public land tenure, long-term forestry and grazing leases. Increasing intensity and frequency of disturbance processes due to climate warming and landscape management.	Mosaic of old-growth forest, secondary forest, and selectively logged forest, agroforestry practices ("chakras"). Increasing urbanization, intensive agriculture, and infrastructure development. Selective logging and illegal hunting remain an issue. Subsistence hunting decreasing. Production and export (cacao, *Ilex guayusa*) increasing. High poverty. Environmental and territorial planning are undeveloped.	Forest embedded in mosaic of small-holder farms and large multinational tree plantations, high poverty and history of social oppression, low levels of land tenure, lawlessness, farmers use forest for wood, firewood, water, illegal hunting, investment. Indigenous Mbya people marginalized and struggling to sustain their livelihoods.	Forest primarily on mountain slopes, interspersed with grasslands and shrublands. Valleys occupied by agricultural fields, native forest fragments of diverse sizes, exotic tree plantations, lakes and rivers. Agroforestry systems from indigenous Mapuche communities, campesinos, and new settlers are interspersed with large ranches and, increasingly, urban areas.

[1] Martin et al. (2004), Drever and Martin (2007).
[2] Perz et al. (2005), Torres et al. (2015), Dueñas et al. (2016).
[3] Rau (2005), Ríos (2006).
[4] Armesto et al. (2010), Echeverría et al. (2012), Barreau et al. (2016), Caviedes and Ibarra (2017).

Fig. 3. In this panarchy model of nest web patterns and processes interacting across spatial and temporal scales, the continuous reshuffling within adaptive cycles at each level, and the constant feedback across levels, allows the nest web to constantly adapt and evolve to the changing conditions of forests around the world (see Table 1 for details).



dispersers, e.g., toucans and parrots, and large-seeded animal-dispersed trees (Tabarelli et al. 1999, Lammertink et al. 2019). This process of change, with the evolving community of trees, excavators, and nonexcavators, constrains and stabilizes the smaller and faster processes of recruitment, decay, and loss of cavities at the single nest-tree level. The nest web is also sensitive to and evolves according to processes that influence the species pool and disturbance regimes at higher level adaptive cycles (landscape and regional levels, below; Cockle et al. 2019*a, b*).

Landscape mosaic of nest webs

At the landscape level, variation in forest disturbance and regeneration patterns and processes lead to a shifting mosaic of forest patches (stands) along with growth (r) or recruitment of a range of nest web communities. Fire and other social-ecological disturbance regimes, driven for instance by climate change, market forces, and policy pressures, create patches of various sizes and age class distributions that generally follow a scale-free pattern (Perry et al. 2011, Filotas et al. 2014), which we hypothesize will influence the landscape pattern of nest web communities. The conservation (K) stage in the community of interacting nest webs occurs when the shifting mosaic of forests across the landscape reaches a dynamic equilibrium. Rapid release (Ω) of the nest web structure can occur when a large scale, infrequent disturbance causes extensive tree mortality, shifting forest composition and age, as when mountain pine beetle (*Dendroctonus ponderosae*) kills extensive areas of lodgepole pine forest across the British Columbia landscape on a return interval

of 30–40 years (Alfaro et al. 2010, Simard et al. 2013, Cockle and Martin 2015). In the most recent outbreak, death of lodgepole pine (*Pinus contorta*) and release of trembling aspen (*Populus tremuloides*), for example, caused a rapid reorganization (α) of the community of nest webs across the landscape. This rapid reorganization at the landscape level, coupled with the changing climate, led to a high degree of unpredictability and uncertainty in the recovering forest structure, and fluctuations in abundance and fecundity of several species in the nest web (Edworthy et al. 2011, Norris and Martin 2014). The evolving mosaic of forests and interacting nest webs across the landscape influences the composition of nest webs at the (lower) stand level, and vice versa (Drever and Martin 2007, Norris and Martin 2014). As a consequence of the landscape level disturbance, release (Ω) and reorganization (α) lead to reorganization of the nest web, allowing the possibility of novel species and links (Martin et al. 2006, Cockle and Martin 2015).

Regional mosaic of nest web landscapes

At the regional level, historical evolutionary processes, the distribution of biomes according to climate, and other social-ecological (including economic and political) forces have determined the distribution of cavity-nesting species and their interactions in nest webs across latitudinal and longitudinal gradients leading to growth (r) of different nest web landscapes in boreal, temperate, and tropical regions (Bai et al. 2003, Martin et al. 2004, Cooke and Hannon 2011, Cockle et al. 2011, 2019*b*, Altamirano et al. 2017). A relatively stable climate in the past centuries may have resulted in conservation (K) of the distribution of nest webs across the Americas. However, with recent changes in land-use patterns, as well as species invasions and widespread wildfires, and concomitant changes in forest cover, health, and tree species ranges, the global distribution of nest webs is vulnerable to rapid shifts or releases (Ω). Climate change, defaunation, and rapid expansion of human-modified landscapes, including land intended for satisfying an increasing demand for timber, paper, or pasture land, and replacement of large proportions of native forest with non-native tree plantations, will likely lead to massive reorganization (α) of nest webs across regions (Tabarelli et al. 1999, Harley 2011, Ibarra and Martin 2015, Van der Hoek et al. 2017).

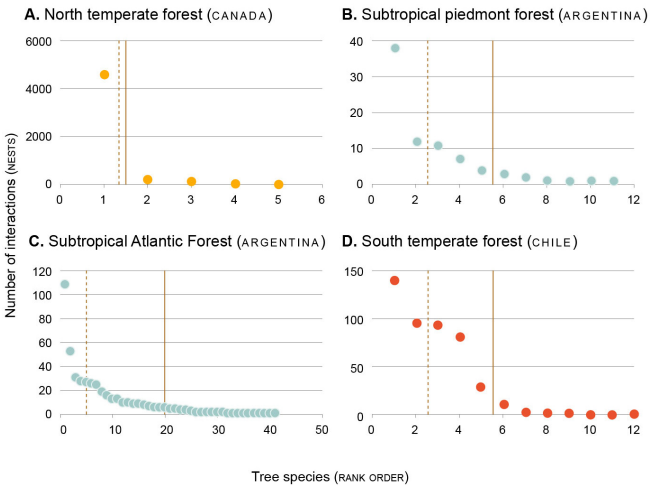
PROPERTIES OF NEST WEBS AS COMPLEX ADAPTIVE SYSTEMS

Redundancy and heterogeneity

Redundancy describes the replication of pathways in a system, and is determined by the number of entities that perform a particular function similarly (Walker 1992, Biggs et al. 2015). Redundant entities in nest web systems can include, for example, individual cavities and species (plants, excavators, decay organisms, seed dispersers, mycorrhizal fungi). Changes in cavity supply are likely to have the greatest impact on nest webs where cavities are scarce (low redundancy) and limit breeding density, e.g., subtropical Atlantic Forest (Cockle et al. 2010, Lammertink et al. 2019). Across species, the cavities produced by excavators in our systems vary in size by an order of magnitude, from 3.1 cm² entrance area (12 g Ochre-collared Piculet *Picumnus temminckii*) to 225 cm² (260 g Magellanic Woodpecker *Campephilus magellanicus*). Low species redundancy occurs in the south temperate forest (Chile), where only four species of excavators produce cavities, overlapping very little in size, i.e., restricted niche available to nonexcavators (Ibarra and Martin 2015, Altamirano et al. 2017); high redundancy occurs in our north temperate forest (Canada), subtropical forest (Argentina), and tropical forest (Ecuador) study areas, where 12–17 excavator species produce cavities that partially overlap in size, and in some cases are used interchangeably by nonexcavators, likely increasing the resilience of the nest web (Cockle et al. 2011, 2019*b*, Cockle and Martin 2015, Van der Hoek and Martin 2018).

Nest web heterogeneity occurs at multiple levels. At the smallest level, wood hardness and decay organisms are distributed heterogeneously within individual trees, determining where and when birds can excavate a cavity (Larrieu et al. 2014). At the nest web community level, a few tree species represent key network hubs, with < 20% of tree species accounting for > 50% of nests, and < 50% of tree species accounting for > 90% of nests (Fig. 4), a nonlinear, approximately scale-free pattern common to many complex systems (Parrott and Meyer 2012). At the landscape level, nest webs can exhibit high values of beta diversity, as cavity abundance and nest web composition vary with elevation and disturbance history (Fig. 4A; Politi et al. 2012, Ibarra et al. 2017*b*, Van der Hoek and Martin 2018), influencing nest web structure and function (Robles and Martin 2014). Across regions, we find heterogeneity in the components, diversity, and structure of nest webs. Whereas nest webs in North America exhibit low interaction evenness, depending primarily on cavities created by excavators in standing trees of one or two species (Martin et al. 2004, Blanc and Walters 2008*b*, Cooke and Hannon 2011), those in tropical, subtropical, and temperate forests of South America exhibit higher interaction evenness and involve a more diverse array of

Fig. 4. Across multiple nest webs, interactions are disproportionately distributed, with < 20% of tree species accounting for > 50% of nests (dashed vertical line), and < 50% of tree species accounting for > 90% of nests (solid vertical line). Data sources: Ruggera et al. (2016); T. A. Altamirano and J. T. Ibarra (*unpublished data*), K. L. Cockle (*unpublished data*), K. Martin (*unpublished data*).

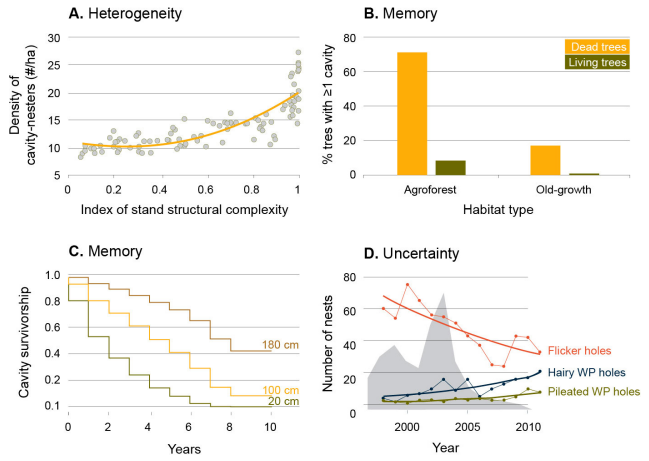


cavity substrates, including many tree species, palms, bamboo, tree ferns, arboreal termite nests, and fallen trees (Cockle et al. 2012, 2019*b*, Altamirano et al. 2017, Van der Hoek and Martin 2018). Logging can result in disproportionate biodiversity losses especially when key hubs (tree species or sizes) are targeted; however, high redundancy of species or functions likely increases resilience of the nest web (Cockle et al. 2010, Ruggera et al. 2016, Ibarra et al. 2017*a*).

Memory

The past conditions of a tree, forest, landscape, or regional biome, including historical land use practices, will have a legacy effect on the types of cavities that are produced, how long they last, and how species interact around this resource (Fig. 5B, C). Large decaying and standing dead trees retain the memory of past forest conditions in their wood properties and canopy structure (Briffa 2000), and are most likely to generate cavities for a range of vertebrate fauna (Blanc and Martin 2012). In many systems, cavities in living trees may persist for several decades (Lindenmayer and Wood 2010, Wesołowski 2012, Cockle et al. 2017; Fig. 5C), during which they can be used > 20 times by nesting vertebrates (Cockle et al. 2019*a*).

Fig. 5. Properties of nest webs for different study systems in the Americas. (A) Heterogeneity (Chile): stands with a dense understory, large-decaying trees, and a deep leaf-litter create microhabitats (structural complexity) not only for cavity nesters, but also for insects and small mammals, the main food items for several cavity nesters (Caviedes and Ibarra 2017; J. T. Ibarra, *unpublished data*). (B) Memory (Ecuador): agroforests sustain habitat legacies (standing dead trees) that are highly used by excavators. They have a disproportionate impact on cavity-nesting community composition (Y. Van der Hoek, *unpublished data*). (C) Memory (Argentina): tree-cavity persistence increases with tree size, so that large old-growth trees have a longer legacy (Cockle et al. 2017). (D) Uncertainty (Canada): woodpecker (WP) populations increased during and after an insect outbreak (grey area). Nonexcavators switched from Northern Flicker (*Colaptes auratus*) cavities to cavities created by a broader suite of woodpeckers, leading to changes in nest web architecture, including increased evenness (Cockle and Martin 2015).



Although cavities are hosted by individual trees, the memory processes of these individuals are derived from interaction networks with other organisms at larger scales. For example, forest patches surrounding a recently disturbed area will supply sources of memory, often vectored by mobile linkages, e.g., seed and spore-dispersing animals, that speed up regeneration (Filotas et al. 2014). A single fire event can influence habitat legacies for one or several centuries, for example, by destroying all existing cavities, by dramatically altering stand structure and composition, or by creating high densities of standing dead trees (Dansereau and Bergeron 1993, Lindenmayer et al. 2012). In Chile, standing dead trees increase forest-stand structural complexity (Caviedes and Ibarra 2017) and positively influence breeding site selection and fecundity of cavity nesters (Altamirano et al. 2017; Fig. 4B). Currently, legacy trees from previous centuries sustain cavity-nesting communities in many secondary forests, partially logged forests, and agricultural landscapes, where cavity-using vertebrates would not otherwise be able to persist (Fischer et al. 2010, Lindenmayer et al. 2014, Ibarra et al. 2017*a*).

Uncertainty and nonlinearity

Nest webs can be a useful tool for predicting the effects of disturbance on avian community structure (Blanc and Walters 2007), but their spatio-temporal dynamics are also riddled with uncertainty. Biotic, e.g., insect outbreaks, abiotic, e.g., fires or volcanic eruptions, and anthropogenic, e.g., logging or human-induced fires, forces can modify the structural and functional attributes of nest web systems in unforeseen ways (Filotas et al. 2014, Ruggera et al. 2016), resulting in shifts in nest web architecture and nonlinear responses to disturbance. For example, where selective logging removed half the basal area of trees from subtropical forests in Argentina, the cavity-nesting community responded nonlinearly with nine times fewer cavities and 17 times fewer nests in logged areas than in old-growth forests (Cockle et al. 2010).

Sources of uncertainty in the system not only reduce our ability to predict the future state of nest webs, they also generate variability that may be amplified by feedback loops, leading to the emergence of novel relations or links among species. When nest webs in western Canada experienced an outbreak of mountain pine beetle, the keystone species in the excavator guild changed from Northern Flickers (*Colaptes auratus*) before the outbreak, to a broader suite of less common woodpeckers, increasing network evenness and decreasing nestedness (Cockle and Martin 2015; Fig. 4D). Then, fires destroyed many cavities, and flickers increased their excavation rate by more than 30% (Wiebe 2014, 2017), suggesting that flickers (and other abundant excavators) may play a key role in regulating cavity supply. Research on the long-term dynamics of nest web systems at multiple levels would help reduce uncertainty about their responses to social-ecological disturbances.

CONCLUSION: NURTURING RESILIENT NEST WEBS

Linkages among nest web entities (individuals, species, guilds), functioning of interacting adaptive cycles, i.e., panarchy, and properties resulting from their interactions, are key factors contributing to the resilience of forest communities. Heterogeneity, redundancy, and memory allow nest web systems to absorb some degree of disturbance without undergoing a regime shift, that is, without changing the basic structures and functions, and thus the identity, of nest webs.

We recommend that forest and wildlife ecologists, managers, and public agencies charged with forest biodiversity conservation attempt to define thresholds at which nest web systems are no longer considered resilient, i.e., basic structures and functions—system's identity—are altered (Holling 1973, Walker and Salt 2006). Although quantifiable, thresholds are frequently set according to human values (Messier et al. 2013, Biggs et al. 2015), and vary depending on the adaptive cycle under consideration for management intervention. We suggest that a future research agenda on nest webs should include an assessment of thresholds and should explicitly contemplate human institutions shaping nest web systems, so that the panarchy can be understood as a coupled social-ecological system (Holling 2001). A social-ecological research agenda will allow better and more realistic assessments of how nest web dynamics and possible futures are shaped by the pressure from multiple stakeholders and policy makers acting at local, national, and international scales (Filotas et al. 2014). This applied research agenda will also enable increasingly sophisticated forest management that attends several adaptive cycles, at the individual tree or community levels, and also above to the landscape and regional levels.

Studying and managing forests to sustain nest web resilience will require attention to the full panarchy of the adaptive cycles. For example, a study using a panarchy framework on reindeer (*Rangifer tarandus*) husbandry shows the incongruence between forest management across different levels: the management scale of a large forest company is that of their land holdings within a region (varying from < 10 ha to a few hundred ha) while, on the other hand, the management scale of one reindeer herding district involves the landscape used by a winter herding group during a decade or more (several tens of thousands of ha; Moen and Keskitalo 2010). In this case, it is critical to embrace a multilevel perspective from the lichen (feeding) resource to a rotational use of grazing lands in relation to the dynamics of the animals and variations in weather, to increase their buffering capacity that maintains resilience in their resource use (Sandström et al. 2006).

In a nest web context, it is critical to maximize memory focusing on what is retained, what is removed (Gustafsson et al. 2012, Mori and Kitagawa 2014, Baker et al. 2015), and what can be developed through forestry practices in adaptive cycles, from individual trees to regions. We need to find locally acceptable ways to retain and recruit large trees, ensure a variety of tree densities and species compositions in the landscape, and manage regional land-use and disturbance regimes to ensure a representative mosaic of forests (Lindenmayer and Laurance 2017, Koch and Munks 2018). In our study area in subtropical forests of Argentina, the national "Ley de Bosques Nativos" (Law 26331) and associated territorial planning under Provincial Law XVI N° 105 were followed by reduced annual deforestation rates at the provincial level (30,000 km^2). However, these laws are insufficient, alone, to conserve representative cavity-nesting communities because selective logging of stands on unsustainable cycles (< 20 years) leaves impoverished forests where timber is not worth harvesting legally, and large degraded forest properties are slowly abandoned to illegal logging and unregulated deforestation for small-scale tobacco farming (Manzanal and Arzeno 2011, Campanello et al. 2019). To conserve a representative diversity of nest webs, finer scale policies are needed to address critical social-ecological concerns at the scale of individual forestry operations and small farming properties (20–100 ha) that dominate under-represented cavity-nesting assemblages, such as those of Araucaria forests (Cockle et al. 2019*b*).

Specific management needs will vary across nest web systems. A great challenge for managing to nurture resilience in social-ecological systems, in this case nest webs in forests, is that the governance of different countries and regions face different sources of uncertainty and historical and contemporary issues, e.g., political and socioeconomic (Messier et al. 2013). We must thus understand both the internal dynamics within each country and region, and the interactions among stakeholders to assess and hopefully nurture the resilience of the system as a whole. In subtropical Argentina and south temperate Chile, specifically, we suggest it is critical to rethink current forest policies (or the lack of them) that simultaneously (1) promote large monoculture tree plantations, and (2) degrade native forest through unsustainable ("high-grade") logging operations that overwhelmingly remove the largest living trees with greatest value to biodiversity (Cockle et al. 2012, 2015, Ibarra et al. 2017*a*). At the same time, forest and farm management could take advantage of nest web resilience by ensuring that nonexcavators have opportunities to switch to the relatively ephemeral woodpecker cavities in smaller and fast-growing trees, and ensuring that the landscape is sufficiently heterogeneous and redundant to provide foraging and nesting resources year round. For example, at our study area in Canada, nonexcavators most often use cavities excavated by woodpeckers in trembling aspen (95%; Martin et al. 2004, Cockle et al. 2011). Logging operations in this region retain most aspen and large Douglas fir (*Pseudotsuga menziesii*), reducing tree density but conserving the key habitat structures for cavity-using vertebrates, i.e., retaining nest web memory. The nest web is resilient to these practices, but current shifts toward clear-cutting, herbicide spraying, and planting monocultures in the lower elevation Douglas fir forest could rapidly undermine this resilience.

Managing disturbance regimes and protecting the shifting mosaic of different ages and composition of forests in the landscape, as well as mitigating climate shifts and attending to colonization of species at the biome level, will ensure a much more robust system of forest biodiversity than is possible with the historic management focus at the tree and forest community levels. Acknowledging the complexity, both ecological and social, of nest web systems may also help researchers and forest managers effectively communicate their management recommendations to the public (Parrott and Meyer 2012). Management and policies at all levels should aim to nurture resilience in relation to long-term adaptive conservation objectives in an uncertain future.

Responses to this article can be read online at:
http://www.ecologyandsociety.org/issues/responses.php/11590

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