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Natural disturbance regimes for implementation of ecological forestry: a review and case study from Nova Scotia, Canada

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Abstract

Ecological forestry is based on the idea that forest patterns and processes are more likely to persist if harvest strategies produce stand structures, return intervals, and severities similar to those from natural disturbances. Taylor et al. (2020) reviewed forest natural disturbance regimes in Nova Scotia, Canada, to support implementation of ecological forestry. In this follow-up paper, we 1) review use of natural disturbance regimes to determine target harvest rotations, age structures, and residual stand structures; and 2) describe a novel approach for use of natural disturbance regimes in ecological forestry developed for Nova Scotia. Most examples of ecological forestry consider only the local, dominant disturbance agent, such as fire in boreal regions. Our approach included: 1) using current ecological land classification to map potential natural vegetation (PNV) community types; 2) determining cumulative natural disturbance effects of all major disturbances, in our case fire, hurricanes, windstorm, and insect outbreaks for each PNV; and 3) using natural disturbance regime parameters to derive guidelines for ecological forestry for each PNV. We analyzed disturbance occurrence and return intervals based on low, moderate, and high severity classes (<30, 30-60, and >60% of biomass of living trees killed), which were used to determine mean annual disturbance rates by severity class. Return intervals were used to infer target stand age-class distributions for high, moderate, and low severity disturbances for each PNV. The range of variation in rates of high severity disturbances among PNVs was from 0.28% yr⁻¹ in Tolerant Hardwood to 2.1% yr⁻¹ in the Highland Fir PNV, equating to return intervals of 357 years in Tolerant Hardwood to 48 yrs in Highland Fir PNVs. As an example, this return interval for the Tolerant Hardwood PNV resulted in target rotation lengths of 200 years for 35% of the PNV area, 500 years for 40%, and 1000 years for 25%. The proposed approach of determining natural disturbance regimes for PNV communities and calculating target disturbance rates and corresponding harvest rotation lengths or entry times appears to be a feasible method to guide ecological forestry in any region with a strong ecological land classification system and multiple disturbance agents.

Key words: natural disturbance, ecological forestry, sustainability, potential natural vegetation, ecological land classification, landscape planning

1. Introduction

Ecological forestry (also known as ‘ecosystem-based forestry’) emphasizes the conservation of native biodiversity and ecological integrity (Christensen et al. 1996; Seymour and Hunter 1999). At the core of ecological forestry is the idea that natural forest patterns and processes, including both biodiversity and forest productivity, are more likely to persist or be best approximated by designing and applying forest management strategies and silvicultural systems that ‘emulate’ natural disturbance regimes (Landres et al. 1999; Seymour and Hunter 1999; North and Keeton 2008; D’Amato et al. 2018; Kuuluvainen et al. 2021). Ecological forestry may be distinguished from more economic-driven models of forestry, such as ‘Sustained Yield Forestry’ or ‘Production Forestry’, by its strong focus on the maintenance of natural forest patterns and processes, within which the sustainable provision of goods and services to meet human needs can be achieved (Christensen et al. 1996; Seymour and Hunter 1999; Davis et al. 2001; Burton et al. 2006). Although the concept of ecological forestry has been proposed for many years (e.g., Spurr and Cline 1942; Franklin 1989), jurisdictions across North America have only recently taken serious steps towards its implementation (Long 2009; Kuuluvainen and Grenfell 2012). One of the major impediments has been difficulty developing ecologically rigorous, yet socioeconomically acceptable, management frameworks to emulate natural disturbances.

Ecological forestry was summarized by Palik and D’Amato (2017) as a framework for management, based on several foundational principles, including structural and compositional complexity at multiple spatial scales, ecologically appropriate timing of silvicultural interventions, and objectives developed at landscape spatial scales. The concept of ecological forestry stems from the ‘coarse-filter’ hypothesis of biological conservation (Hunter et al. 1988), which assumes that by using natural disturbances as a template for forest management and silviculture, one will, by default, create and maintain the types of habitats that would have formed naturally in the past, and in so doing, conserve most native species that have adapted to these habitats and their associated ecological processes (Hunter et al. 1988; Landres et al. 1999). Kuuluvainen et al. (2021) thoroughly reviewed the development, ecological and evolutionary foundations, and applications of natural disturbance-based forest management, with emphasis on boreal forests. They concluded that use of natural disturbance regimes in management provides a comprehensive ecosystem-based framework for managing forests for human needs, while also maintaining forest health under a changing environment.

There are several challenges to successful ecological forestry. Foremost is the challenge of sufficiently understanding the natural disturbance regime one wishes to emulate. While it has long been known that all forests are shaped, to varying degrees, by natural disturbances (e.g., Thoreau 1860; Clements 1916; Watt 1947), it is only in the last several decades that jurisdictions in various regions have

begun to invest seriously in research characterizing local natural disturbance regimes for ecological forestry (North and Keeton 2008; Kuuluvainen and Grenfell 2012; Taylor et al. 2020). To describe and understand the effect of a disturbance regime on a particular forest type or region requires knowledge of specific disturbance regime parameters, including: 1) the major natural disturbance ‘agents’ that affect that forest; and 2) their i) spatial extent, ii) severity, and iii) return intervals (Pickett and White 1985; Seymour and Hunter 1999; Bergeron et al. 2002—See definitions in section 2.1). Each of these disturbance regime agents and parameters has a natural range of variability, defined as the ecological conditions, and spatial and temporal variation in these conditions, that are relatively unaffected by people, within a period of time and geographical area appropriate to an expressed goal (Landres et al. 1999). Characterizing natural variability helps to understand how disturbance driving processes vary from one site to another, how these processes influenced ecological systems in the past, and how these processes might influence ecological systems today and in the future (Landres et al. 1999). Characteristics of disturbance regimes are particularly important in generating this natural variability at different spatial and temporal scales (Cyr et al. 2009). Once sufficient information on natural disturbance regimes is known, forestry planners need to determine the best way to use this information to design and apply silvicultural systems and forest management strategies that ‘emulate’ natural patterns and processes (Seymour and Hunter 1999; Kuuluvainen and Grenfell 2012; D’Amato et al. 2018). Other challenges include determining what forest metrics are most important to emulate, determining how to do it, and accounting for climate change and its impacts on forest ecosystems.

Although there are a growing number of examples of the use of natural disturbance regimes in support of ecological forestry across North America, Scandinavia, and other regions, approaches vary considerably in detail and methodology, as jurisdictions attempt to balance social, economic, and ecological constraints (Burton et al. 2006; Long 2009; Kuuluvainen and Grenfell 2012). Most examples of ecological forestry consider only the local, dominant disturbance agent as a basis, with fire being the most common, but also wind (e.g., Kern et al. 2019) or insects (Hennigar and MacLean 2010; Dhar et al. 2016). For example, although varying approaches to ecological forestry have been applied across North America’s boreal forests (Burton et al. 2006), most rely on regional fire return interval as the basis for managing the landscape to achieve specific stand structures, age classes, and compositions (e.g., Hunter 1993; Johnson et al. 1998; Burton et al. 1999; Bergeron et al. 2002; Lafleur et al. 2018). Natural disturbance-based management patterned principally on fire is also common across the western U.S. (North and Keeton 2008). Other examples of management centered on a single, dominant disturbance agent include strategies to control mountain pine beetle (*Dendroctonus ponderosae*) in western Canada (e.g., Alberta Sustainable Resource Development (ASRD) 2007; Dhar et al. 2016), or eastern spruce

budworm (*Choristoneura fumiferana*) outbreaks in the spruce-fir forests of Quebec and New Brunswick (Baskerville 1975; Blais 1983; Hennigar and MacLean 2010).

While models that focus on a single disturbance agent may suffice in situations where one agent dominates, such approaches are less suited to implementing ecological forestry in settings where more complex disturbance regimes exist. Examples of ecological forestry that integrate multiple disturbances are less common (Kuuluvainen and Grenfell 2012), but include Bouchard et al. (2008), Arsenault et al. (2016), and DeGrandpre et al. (2018), who studied fire, wind, and insect outbreaks in parts of eastern Canada; and Lorimer and Frelich (1994), Seymour et al. (2002), Lorimer and White (2003), Seymour (2005), Keeton (2006), D'Amato et al. (2018), and Thom and Keeton (2020) who investigated the complex natural disturbance regimes of northern temperate forests of northeastern North America. In almost all cases, however, the authors acknowledge that one of the greatest challenges to successfully basing management on multiple natural disturbances is acquiring reliable baseline data on specific disturbance agent regimes and accounting for potential interactions and overlap between disturbances. Consequently, most attempts at ecological forestry that consider multiple disturbances tend to be quite generalized, often lacking specific quantitative frameworks for translating natural disturbance regime parameters into applicable forest management guidelines.

As a prelude to this paper, Taylor et al. (2020) completed a comprehensive synthesis of over 300 years of literature and available data to document and interpret the natural forest disturbance regime parameters (i.e., agents, extent, severity, and return interval) of Nova Scotia, Canada, to support implementation of ecological forestry. This was in response to increasing public pressure to return the forests of Nova Scotia to a state more representative of conditions that existed before widespread anthropogenic disturbances (i.e., often thought of as prior to European settlement (*ca.* 1600s), before land-clearing and industrial forestry), while also accommodating competing socioeconomic interests like maintaining adequate wood supply (Nova Scotia Department of Natural Resources (NSDNR) 2011; Lahey 2018). Taylor et al. (2020) concluded that fire, wind (predominantly hurricanes), and outbreaks of spruce budworm were the most important disturbance agents, and quantified areas of low-, moderate-, and high-severity disturbances for each. For example, the mean annual disturbance rate of moderate- to high-severity fire ranged between 0.17% and 0.4%·yr⁻¹ (return interval of 250–600 years), depending on ecosystem type. In this follow-up paper, building on Taylor et al. (2020), we present a novel approach to apply natural disturbance regime parameters to derive ecological forestry management guidelines that target harvest rotations, age structures, and residual stand structures (Fig. 1). This includes: 1) using the current ecological land classification system of Nova Scotia (Neily et al. 2017) to determine and map potential natural vegetation (PNV) community types (Tuxen 1956, Loidi and Fernandez-Gonzalez 2012);

2) determining natural disturbance regimes for each PNV based on findings of Taylor et al. (2020) and supplementary analyses; and 3) using the PNV natural disturbance regime parameters to derive forestry guidelines, using pooled multi-rotation models based on disturbance return intervals, that support development of forest management strategies and silvicultural prescriptions in Nova Scotia. Given the anthropogenic changes in forests over the past centuries in Nova Scotia, knowledge of pre-European settlement forest conditions provides an important ecological benchmark of the degree of change to date for forest management planning (Pinto and Romaniuk 2004), albeit with the recognition that climate change will result in ongoing alteration. Maintaining biodiversity and natural ecological structures and processes may be the best way to ensure the forest can adapt to climate change. Thus, forest managers must determine which natural disturbance regimes are important in their management area, based on records of historical occurrences, but also based on predictions of future changes in disturbance and forest dynamics (Perera and Buse 2004). We begin by first reviewing key principles to consider when attempting natural disturbance-based ecological forestry, and then showcase a novel approach of ecological forestry developed specifically for Nova Scotia.

2. Principles of Ecological Forestry

2.1 Natural Disturbance Regime Parameters

In forest ecology, disturbances refer to events causing tree damage and mortality, which release growing space and resources (Pickett and White 1985). Concepts and terms used in characterizing disturbances are summarized in Table 1. Although many metrics have been used to characterize natural forest disturbance regimes (e.g., White and Pickett 1985; Seymour et al. 2002; Lorimer and White 2003; DeGrandpre et al. 2018), most are based on three main parameters (Table 1): 1) spatial extent, which defines the total landscape area over which a single event (episode) from a particular disturbance agent occurs; 2) severity, which describes the intensity of mortality caused by a disturbance agent and can be quantified by the total amount of living tree biomass killed per unit of forest area during a single disturbance agent event; and 3) return interval, the time elapsed (average or ideally the distribution of times) between successive disturbance agent events of a particular severity, at the same place on the landscape (Taylor et al. 2020). Return interval may also be used to calculate on an annual basis the ‘mean annual disturbance rate’ (MADR), which is the amount (usually expressed as a percentage) of ‘eligible’ forest area disturbed per year by a specific disturbance agent and severity level. Here, eligible signifies that not all forest areas within a landscape are vulnerable to each disturbance. Some disturbance agents are tree species-specific, such as certain insect outbreaks, and only affect forest areas that include host tree species for that insect, while other disturbance agents such as wind or

hurricanes have heterogeneous impacts due to topography and chance, or may vary by species and other factors. Each disturbance regime parameter may be characterized by the mean and range of values characteristic of each natural disturbance agent unique to a forest landscape.

2.2 Summarizing Natural Disturbance Regime Parameters

One of the first steps in ecological forestry is to summarize parameters into ecologically meaningful disturbance regime categories (Seymour and Hunter 1999; Long 2009; Kuuluvainen and Grenfell 2012). This is particularly relevant when a forest has multiple natural disturbance agents, and each episode may vary considerably in its spatial extent and severity (e.g., severe stand-replacing windthrow versus partial windthrow originating from a single hurricane), as well as where and how such agents vary by stand type.

To help simplify possible scenarios, researchers have used a variety of systems to summarize unique combinations of natural disturbance regime parameters, from simple categorizations that merely discriminate between major versus minor stand disturbances based on severity, to more elaborate schemes that categorize according to multiple disturbance regime parameters (Roberts 2007). The disturbance categorization used by Taylor et al. (2020) was based on three classes each of spatial extent (>500ha, 500-50ha, <50ha), severity (>60% mortality, 60-30%, <30%), and return interval (>150 years, 150-50 years, <50 years), plus the MADR (% yr⁻¹). These classes were chosen to reflect stand-level, multi-stand, and regional spatial extents; individual-tree, partial stand, and majority of stand living tree biomass killed; and short, medium, and long-term return intervals, relative to stand harvest interventions in the region (Taylor et al. 2020). This was an attempt to provide enough categories to capture variation in disturbance behavior among agents and be simple enough for practical implementation by forest managers, to align with existing management guidelines in Nova Scotia.

2.3 Using Disturbance Regime Categories to Inform Decision Making

Seymour and Hunter (1999) provided a basic framework for how to use natural disturbance regime categories to inform forestry decision making. Most forestry decisions occur at either the forest stand or landscape spatial scale (Burton et al. 1999; Davis et al. 2001; Harvey et al. 2002). A stand is usually the basic operating unit for silviculture and forest management and is defined as a typically 1-100 ha sized area containing a group of trees sufficiently uniform in species composition, density, and age class structure that it can be differentiated from adjoining forest areas (Davis et al. 2001; Ashton and Kelty 2018). A forest landscape is a typically 10³-10⁶ ha mosaic of forest stands and non-forested ecosystems (Smith and Smith 2015; Ashton and Kelty 2018). From a forestry standpoint, a landscape is managed as a collection of forest stands, administered as a single, integrated forest planning unit (Davis et al. 2001), at least for large ownerships or Crown land. The treatment of individual stands (i.e.,

growing, tending, and regenerating) is the domain of ‘silviculture’, while the process of stocktaking, regulating, and scheduling activities on stands within the landscape is ‘forest management’.

The ‘stand-to-landscape’ spatial framework is useful for the application of natural disturbance regime parameters for designing and applying silvicultural systems and forest management strategies (Long 2009). Seymour and Hunter (1999) listed key stand- and landscape-level decision points: at the stand level: i) determining the appropriate age structure and species composition of trees within stands (e.g., single-aged versus multi-aged stands), ii) scheduling cutting activities (i.e., harvest rotation length, in the case of severe disturbances and clearcuts, or entry times in the context of partial harvests), iii) determining the method of regeneration, and iv) implementing protocols for maintaining and/or restoring essential stand-level biodiversity features and ecosystem functions; and at the landscape level: v) determining the age structure and species composition of stands on the landscape, vi) calculating the overall annual sustainable harvest; and vii) implementing protocols for maintaining, augmenting, or restoring ecological integrity, ecosystem function, and representative biodiversity.

2.3.1 Stand-level decisions

Silviculture is used to emulate natural disturbance through cutting activities and manipulation of stand age class structure. Depending on severity of the disturbance, different age class structures will result (MacLean and Ostaff 1989; Kneeshaw et al. 2011; Taylor et al. 2013; Waldron et al. 2013). A single, high severity disturbance event (e.g., intense crown fire or strong wind) will usually kill most trees in a stand (Foster and Boose 1992; Haeussler and Bergeron 2004; Bouchard et al. 2009; Taylor et al. 2017a; Walker et al. 2019), therefore initiating a predominantly ‘single-aged’ stand (only one age class present) or ‘multi-aged’ (two to three distinct age classes) stand structure (Ashton and Kelty 2018). In contrast, repeated episodes of less severe disturbances (e.g., low-to-moderate severity windstorms or insect outbreaks affecting only selected species, and/or having less impact), that kill fewer trees per disturbance event, will leave behind a greater abundance of standing live trees, and contribute to gap dynamics and/or development of more complex ‘all-aged’ stand structures in which four or more age classes of trees may coexist (Runkle 1991; Lorimer and Frelich 1994; McCarthy 2001). Various silvicultural cutting methods promote different stand age class structures, from clearcutting, seed tree, and uniform shelterwood harvests that promote single- and multi-aged stands, to selection methods that encourage development of all-aged stand structures meant to emulate stand gap dynamics (McCarthy 2001; Ashton and Kelty 2018). Under ecological forestry, silviculture should be guided by disturbance agent, severity, return interval, and intended outcome, as well as current stand condition.

Decisions about both the intensity of cutting (e.g., clearcutting versus partial cutting) and timing of cutting should also be guided by natural disturbance regime parameters. Intensity of cutting should

generally replicate the severity of disturbance, defined here as the percentage of living tree biomass killed, to produce similar stand structure and function. Timing of cutting should replicate the disturbance return interval, the time elapsed between successive disturbance events, in order to produce similar stand age distributions across the landscape as natural disturbances. The harvest rotation length for clearcutting (or forms of seed tree and uniform shelterwood methods) is approximated by the return interval of severe natural disturbance (Bergeron et al. 1999, 2001; McRae et al. 2001). For less severe, more frequent natural disturbances, the timing and intensity of cutting entries (Ruel 2020) will be determined based on lower severity disturbances (Angers et al. 2005; Neuendorff et al. 2007; Raymond et al. 2009; Bolton and D'Amato 2011). Also, one should recognize that there are issues of qualitative differences between disturbances beyond disturbance severity and cutting intensity, e.g. fire-related unique microhabitats, charred wood, abundant remaining dead wood after insect outbreaks, etc.

Stand regeneration may vary substantially depending on disturbance agent and severity. For example, regeneration following high severity fire differs fundamentally from that following severe windthrow, including differences in soil substrate conditions, residual stand structure, vegetative reproduction, abundance of advance regeneration, and other effects on biodiversity. Severe fire generally consumes most forest floor organic matter and understorey vegetation, sometimes leaving large live trees (Johnson 1996), and regeneration originates from local seed rain or stump and root sprouts (Haeussler and Bergeron 2004; Johnstone and Kassischke 2005; Jayen et al. 2006). Wind, however, tends to thin from above, with severe wind downing overstorey trees through stem breakage or uprooting, but leaving the understorey and forest floor largely intact (Waldron et al. 2013; 2014; Taylor et al. 2017a). Advance regeneration plays a much larger role in stand recovery following windthrow, with overturning of tree roots contributing to pit-and-mound formation and mineral soil exposure for seed germination. Accounting for these differences in regeneration dynamics through appropriate site preparation (e.g., prescribed burning and scarification) and regeneration method (e.g., natural seeding versus planting) is critical to the success of stand-level ecological forestry (McRae et al. 2001; Ward et al. 2014; Mallik 2003; LaFleur et al. 2018). For example, on forest sites that develop dense aggressive understories (e.g., ericaceous *Rhododendron* and *Vaccinium* species) and thick forest floor organic layers, fire plays a critical role in reducing vegetation competition and maintaining site productivity (Yamasaki et al. 1998; Royo and Carson 2006; Ward et al. 2014). Harvesting such sites without addressing the build-up of dense shrubs and forest floor organic matter can lead to drastic reductions in site productivity (Mallik 2003; Fenton et al. 2005; LaFleur et al. 2018), biodiversity, and retrogression (Peltzer et al. 2010). In addition to regeneration, there are also important stand structure

elements such as amount of standing and downed deadwood, retention of large trees, and size and shape of harvest blocks that should be incorporated into ecological forestry.

2.3.2 Landscape-level decisions

At the landscape level, natural disturbance regimes are used to guide the abundance and distribution of different stand ages across the landscape—which bear directly on annual sustainable harvest (Sedjo 1996; Burton et al. 1999; 2006; LaFleur et al. 2018). ‘Area-based’ determination of annual sustainable harvest level attempts to set harvest rates based on maintaining a specified stand age class structure on the landscape (Davis et al. 2001). Sustained-yield forestry maintains an even distribution of stand age classes, with equal areas of each age class represented up to a specified rotation length age (Fig. 2a). The emphasis is on maintaining a steady wood supply over the long term without much consideration of variability in stand ages over the landscape due to natural disturbance variation (Davis et al. 2001). In contrast, under ecological forestry, the goal is to maintain (or recreate) a stand age-class structure that mimics what would occur naturally as a result of natural disturbances and their inherent return intervals (or MADRs) (Seymour and Hunter 1999; Long 2009; Kuuluvainen and Grenfell 2012).

To illustrate the difference, consider two 10,000 ha, landscapes, with one managed under sustained-yield forestry using clearcutting on a 100-year rotation length and 1% yr⁻¹ annual sustainable cut (i.e., 100 ha yr⁻¹) and the second managed under ecological forestry emulating stand-replacing wildfire (still using clearcutting), but with a 100-year ‘return interval’ and 1% yr⁻¹ MADR. Under the sustained yield model, no stand is permitted to age beyond 100 years old, nor harvested any sooner, resulting in a rectangular, uniform age-class distribution across the landscape (Fig. 2a). Under ecological forestry, 1% of the landscape is still harvested and regenerated each year, but the 100-year ‘return interval’ implies an entirely different age-class structure (Fig. 2b). This is because the concept of return interval considers the quasi-randomness of natural disturbances and represents the ‘average’ time elapsed between successive disturbances at the same place on the landscape, which acknowledges that some stands will burn younger and others will escape fire for longer periods (Seymour and Hunter 1999; Bergeron et al. 2002; Lorimer and White 2003). Van Wagner (1978) proposed that this variation in disturbance behavior would approximate a negative exponential (not uniform) age class distribution across the landscape (Fig. 2b and Equation 1):

$$a(x) = p \cdot e^{-p \cdot x} \quad [\text{Eq. 1}]$$

where $a(x)$ is the proportion of forest area of stand age-class x and p is the MADR (the inverse of the return interval). It is important to note here that stand age in this context refers to ‘time since disturbance’ (TSD), not necessarily the dominant age of trees in that stand. The negative exponential stand age structure results under two key assumptions: all area (stand types and age classes) are equally

likely to be disturbed, and equal area is disturbed each year. While the former may be probable, the latter is less so, as temporal variability in disturbance occurrence is likely to result in varying stand age distributions across the landscape over time, which may deviate somewhat from the hypothetical distribution shown in Fig. 2b. Thus, it should be viewed as an approximation and a guide. Given the high frequency of disturbances from hurricanes, windstorm, fire prior to suppression, and insect outbreaks in Nova Scotia (Taylor et al. 2020), we decided to use the negative exponential age-class distribution. This has also been used for generally similar forest types in Maine, USA (Seymour et al. 1999). Depending on forest type in Nova Scotia, moderate- to high-severity fires had return intervals of 250–600 years, hurricanes make landfall, on average, every 7 years, resulting in wide-scale damage, and spruce budworm outbreaks cause high-severity damage to fir-spruce every 30–40 years (Taylor et al. 2020).

Under a 100-year return interval, approximately 37% of the landscape would be composed of stands greater than 100 years TSD, and 5% of the landscape would be over 300 years TSD. If the return interval increased to 500 years, similar to fire return intervals in parts of eastern North America (e.g., Bergeron et al. 2001; Lorimer and White 2003; Lauzon et al. 2007), the MADR would be reduced to $0.2\% \text{ yr}^{-1}$ and ~5% of the landscape would escape fire for over 3000 years.

The difficulty in applying an area-based control method using return interval, is that landscapes often have more than one natural disturbance agent operating and these occur at differing return intervals, severity levels (e.g., not just stand-replacing events), or only affect certain tree species. To overcome this challenge, we developed a '*multi-rotation model*' (Fig. 2c), where the negative exponential age-class distribution is emulated by allocating portions of the landscape under different harvest rotation lengths. In this example, the grey rectangles represent three portions of the landscape, with 30% managed on a 50-year harvest rotation length, equivalent to $2.0\% \text{ yr}^{-1}$ harvest, 50% on a 150-year rotation ($0.67\% \text{ yr}^{-1}$ harvest), and 20% on a 300-year rotation ($0.33\% \text{ yr}^{-1}$ harvest) (Fig. 2c). Although harvest rates vary among the portions, cumulatively, 1% of the landscape would be harvested each year.

While the '*multi-rotation model*' provides a means of emulating the effects of a single, severe disturbance regime—fire in this case—multiple disturbance agents may occur at varying severity levels. In our Nova Scotia context, this includes the cumulative effects of four major disturbance agents: hurricanes, windstorms, fire, and spruce budworm outbreaks that only affect spruce (*Picea* sp.) and balsam fir (*Abies balsamea* (L.) Mill.) host species, but also low-to-moderate severity disturbances that drive the development of all-aged stands (Taylor et al. 2020). To account for this, the effects of disturbances were pooled by severity level by summing together their respective MADRs at each severity level (e.g., Seymour et al. 2002; Lorimer and White 2003; Bouchard et al. 2008), which we have termed a '*pooled-multi-rotation model*'. For example, if fire and wind were the only two disturbance

agents operating on the landscape, each at only two levels of severity (low and high), then we would have two ‘pooled-multi-rotation models’, similar to the model illustrated in Fig. 2c, for low severity fire and wind and high severity fire and wind. A challenge to this approach is addressing potential overlap between pooled disturbances, such as stands that blow down and also burn, and interactions between disturbances, such as windthrow altering the probability of burning (or vice versa) (Cannon et al. 2017) or windthrow increasing during and following spruce budworm outbreaks (Taylor and MacLean 2009). However, over the long term, such differences may be within the margin of error of the estimated MADRs and not actually matter (Arsenault et al. 2016). Similarly, return intervals here are not precise to the year, but rather are mean estimates and variation can be quantified by range or standard deviation.

3. Study area: Nova Scotia

Nova Scotia is a small province in eastern Canada with approximately 4.3 million ha of forest. Because of its coastal location and complex geology, it has a diverse landscape, including rugged northern highlands, coastal cliffs and beaches, and over 3000 lakes. The province has a cool moist climate shaped by its proximity to the Atlantic Ocean, providing an environment that supports a wide diversity of flora and fauna (McAlpine and Smith 2010). As a peninsula, Nova Scotia has 13,000 km of coastline and considerable coastal-influenced forests.

The combined effects of European settlement since the 17th century, including forest exploitation, clearing for agriculture and settlement, and other land use practices have markedly altered natural patterns of forests in Nova Scotia (Loo et al. 2010). Similar to other jurisdictions in North America, these influences have transformed natural landscape-scale patterns of forest structure, and stand-level species composition, snags, downed wood, and soils (Noseworthy and Beckley 2020). These in turn have been further influenced by fire suppression and changes in the severity and extent of other forest disturbances, disrupting the natural distribution of terrestrial and aquatic habitats, and their functional linkages (Hessburg et al. 2002).

Nova Scotia is part of the Atlantic Maritime Ecozone (Canadian Council on Ecological Areas 2014), and is further categorized into nine provincial ecoregions, ranging in size from 416 km² to 16,870 km² (Fig. 3; Neily et al. 2017), based on distinctive ecological responses to regional climate and physiography. In Nova Scotia, ecoregion variation reflects mixed effects of topography and proximity to the ocean. Ecoregions are classified into finer scale ecological land units—ecodistricts, ecosections, and ecosites—based on distinct patterns of topography, landform, geology, soil, and vegetation. A general description of the Nova Scotia ecological land classification system levels is included in Table A1, and vegetation and natural disturbances in each ecoregion are described in the supplementary material.

4. A Novel Method of Ecological Forestry

4.1 Using ecological land classification to assign potential natural vegetation and natural disturbance regimes

Tuxen (1956) defined PNV as the “*hypothetical natural status of vegetation [. . .] that could be outlined for the present time or for a certain earlier period, by taking away human impact on vegetation.*” To characterize PNV under Tuxen’s definition, an assumption is necessary that the vegetation is in equilibrium with the current climate conditions. Later, Westhoff and van der Maarel (1973) refined the PNV definition as “*the vegetation that would finally develop in a given habitat if all human influences on the site and its immediate surroundings would stop at once and if the terminal stage would be reached at once.*” Although the PNV concept has been criticized (e.g., Chiarucci et al. 2010; Kusbach et al. 2015), many consider it a useful tool for summarizing spatial knowledge to help guide effective conservation and forest management practices (Meidinger and Pojar 1991; Loidi and Fernandez-Gonzalez 2012; Somodi et al. 2012; Roberts 2015; Fore and Hill 2017). Mapping PNV can be descriptive, depicting a ‘natural’ ecological description of extant vegetation types and current environmental factors (Loidi and Fernandez-Gonzalez 2012). Although we recognize that climate change is occurring and will change future forest composition (and this topic will be addressed further in the Discussion), our rationale for using PNV in this study was that changes in Nova Scotia forests to date reflect land clearing, harvesting, and other direct anthropogenic influences other than indigenous presence pre-1600 and climate change. The province has a strong, highly-regarded ecological land classification system (Neily et al. 2017) that is well-suited to spatially estimate PNVs, and we believe that, given anthropogenic changes to many Nova Scotia forest types, PNV better reflects potential “climax” vegetation than current ecosite vegetation classification. Understanding the history of ecological systems (past composition, structure, and spatial and temporal variability) helps managers set goals to maintain and protect ecological systems (Landres et al. 1999).

Vegetation classifications can be applied to existing vegetation or PNV. Existing vegetation classifications are based on the current stage of development, whereas PNV classifications represent the most mature and stable, terminal endpoints of vegetation development, reflecting the integration of climate, topography, and soils (Pfister and Arno 1980). Assigning PNV forest communities and associated natural disturbance regimes to the landscape can be used to approximate the character of forests before European settlement, *ca* 1600 in Nova Scotia, and provide insight into forest conditions with only indigenous human influence. PNV becomes established only if successional sequences are completed without human interference under the present climatic and environmental conditions (Tuxen 1956).

Climate change and the resulting trend towards more severe and frequent natural disturbances (Dale et al. 2001) and altered forest composition (Steenberg et al. 2011; Taylor et al. 2017b) will of course affect these assumptions, which is discussed in Section 5 and is an area for future research.

The focus in PNV assessment is on geographic area and site, where a unique complex of climate-biota-soil-landform results in specific vegetation complexes and ecological functioning (Rowe 1992). Most land classification systems use vegetation to assess similarity of environmental gradients (i.e., elevation, slope, aspect, soil moisture regime, soil nutrient regime, topographic setting, and local climate) and to describe and map zonal and azonal land units (e.g., Loucks 1962; Zelazny 2007; Sperduto and Kimball 2011). Here, zonal refers to sites that have well drained soils with adequate moisture and nutrients for plant growth, while azonal refers to site conditions that limit plant growth, e.g. excessive soil moisture; dry, impoverished soils; severe climatic exposure; organic soils; or shallow soils over bedrock (Baldwin et al. 2019b). PNV forest classifications also include the effects of topography on microclimate (Pfister and Arno 1980). Aerial photo or Lidar analysis can be used to partition units with similar biophysical attributes to which a homogenous PNV layer can be assigned.

Taylor et al. (2020) used the ecoregion level to synthesize natural disturbance regimes because the spatial resolution is fine enough to capture important differences in physiography, climate, and vegetation patterns that influence disturbance regimes (Seymour et al. 2002; Senici et al. 2010; Taylor et al. 2019). However, to assign PNV forest communities, finer spatial resolution of site conditions is required, and therefore the ecosection level was selected. Since the dominant PNVs can be interpreted from ecosections and mapped, it can be used to guide management at both the stand and landscape level; it is analogous to mapped stand type, but based on potential instead of current stand type. Ecosections are distinct subdivisions of ecodistricts that describe enduring physical features e.g., soil drainage, soil texture, topographic patterns, and sometimes landform (Neily et al. 2017). In the Nova Scotia ecological land classification, each ecosection is designated using a four-letter code, where the first letter represents soil drainage, the second letter soil texture, and the third and fourth letters the topographic pattern or landform (e.g., WCHO – well-drained, coarse-textured soils, hummocky landform; see Table 2, Neily et al. 2017). Repeating enduring features of soil drainage, soil texture, topography and (or) landform reinforces the use of ecosections to assign PNV forest communities.

4.2 Ecosection classification methods

The five Nova Scotia ecological land classification system levels and variables used to define each is described in Table A1. Biophysical mapping of Nova Scotia was completed in 1982. Using interpretation of 1:63,360 infrared aerial photography, enduring biophysical features of the landscape were identified and transferred to 1:50,000 maps. Ecosections were defined based on mapped

topographic patterns, soil texture class, and soil drainage class (Table 2). Ecoregions are generally unique, at least within a given ecoregion, where the impact of climate on the enduring physical features is an important factor influencing species occurrence.

During the mapping of biophysical attributes for the land system, soil texture class was determined from soil series mapping, aerial interpretation of landforms, and other available mapping of surficial materials/landforms and bedrock. Soil drainage classes were defined based on a combination of surface run-off and permeability and included rapid, well, moderately well, imperfectly, poorly, and very poorly drained soils. Aerial photographic features, bedrock geology, and surficial geology mapping were used to determine topographic patterns and landforms. Ecosites combine vegetation and soil type, expressing relative soil moisture and soil nutrient conditions (regimes) but as influenced by regional climate, as reflected in ecoregions (Neily et al. 2017). Soil moisture and nutrient regimes are major factors driving forest species composition and development within a climate region (Whittaker 1975; Bowling and Zelazny 1992; Swenson et al. 2012).

Ecoregions may comprise two or more ecosites but typically one ecosite dominates. Theoretically, each of the nine ecoregions in Nova Scotia (Fig. 3; Neily et al. 2017) could have its own unique set of ecosites, but analysis of tree growth data demonstrated that two main ecosite groups occurred, the Acadian (Ecoregions 300, 400, 500, 600, 700, 900, and Ecodistrict 220) and the Maritime Boreal (Ecoregions 100, 800, and Ecodistrict 210) (Neily et al. 2017). A total of 17 Acadian and 11 Maritime Boreal ecosites were identified (Neily et al. 2017), but in this paper, we have combined these 18 ecosites, for the purpose of assigning PNVs, into 10, with six zonal ecosites: Acadian Tolerant Hardwood, Tolerant Softwood, and Tolerant Mixedwood, Maritime Boreal Coastal Spruce-Fir, Coastal Hardwood, and Highland Fir; and four azonal ecosites: Spruce-Pine, Acadian Wet Coniferous, Maritime Boreal Wet Coniferous, and Floodplain (Table 3). Acadian zonal ecosites mainly support shade tolerant and shade intermediate species such as red spruce (*Picea rubens* Sarg.), eastern hemlock (*Tsuga canadensis* (L.) Carriere), sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), and American beech (*Fagus grandifolia* Ehrh.) (Neily et al. 2017). Acadian azonal ecosites typically include species such as black spruce (*Picea mariana* (Mill.) B.S.P.), white pine (*Pinus strobus* L.), red pine (*Pinus resinosa* Ait.), jack pine (*Pinus banksiana* Lamb.), eastern larch (*Larix laricina* K. Koch), red oak (*Quercus rubra* L.), and red maple (*Acer rubrum* L.). Large differences in climate differentiate the Maritime Boreal and Acadian groups. These differences lead to zonal Maritime Boreal ecosites including balsam fir, white spruce (*Picea glauca* (Moench) Voss), black spruce, red maple, and white birch (*Betula papyrifera* Marshall), while yellow birch occurs at transitional locations between Acadian and Maritime Boreal (Neily et al. 2017). Azonal Maritime Boreal ecosites contain mainly black spruce, eastern larch,

and red maple. In azonal and zonal Maritime Boreal forests, tree species associated with early successional communities are similar to those found in later successional forests (Neily et al. 2017).

4.3 Method of assigning PNV forest community to ecosections

We determined characteristic PNV forest species for each ecosection (Fig. 1) using several data sources, including the Nova Scotia Department of Lands and Forestry (NSDLF) Permanent Sample Plot (PSP) database, containing 3250 PSPs (Townsend 2004), and 2500 temporary Forest Ecosystem Classification sample plots (Neily et al. 2013). These plot sources included species lists for trees, saplings, shrubs, and herbaceous vegetation and biophysical site attributes including soil description, parent material, slope position, stoniness, bedrock, aspect, exposure, and microtopography. Plot data were used to develop decision keys of criteria to assign PNVs to each ecosection, based on known soil drainage, landform, ecodistrict, and vegetation information. Other sources of tree distribution data included reports on old forests (Lynds and Leduc 1995; Stewart et al. 2003); historical accounts of forest composition from Nicolas Denys in 1672 (Ganong 1908), Charles Morris in 1761 (Anonymous 1905), Titus Smith in 1801-1802 (Hawboldt 1955), Simeon Perkins in 1766-1812 (Champlain Society 1948), Fernow (1912), and Nichols (1918); and data from the Nova Scotia photo-interpreted forest inventory. Current and older (*ca* 1940) aerial photography, satellite imagery, plot data, and local expert information about vegetation types were used to test and validate PNV decision keys and to help map late successional tree species such as hemlock, white pine, and shade-tolerant hardwoods.

Successional trends toward PNV vegetation can often be identified even in relatively young stands (Pfister and Arno 1980). Compared to Europe, where vegetation has been modified by humans for thousands of years, long-lasting effects of human disturbance on vegetation in Nova Scotia have been pronounced for only two to three hundred years. Human disturbance distributions and intensities are reasonably well known, and enough remnants of original vegetation remain so that direct study is generally possible (Mueller-Dombois and Ellenberg 1974).

Variation in species composition along soil moisture gradients is one of the most striking and well-studied patterns of forest landscapes (Whittaker, 1975; Oliver and Larson 1996). An edatopic grid of tree species occurrence based on soil moisture regime and soil nutrient regime was used to assist in the assignment of PNV to ecosection (Fig. 4, modified from Neily et al. 2017). Neily et al. (2017) used edatopic grids to plot ecosites on axes that corresponded to environmental gradients, and these were modified for Acadian PNVs (Fig. 4a) and Maritime Boreal PNVs (Fig. 4b) based on relative species composition of ecosites and PNVs. Our PNV species-group approach is more applicable to identification and mapping of sites than approaches that incorporate many individual species (Spies and Barnes 1985).

We derived decision keys for each ecoregion to determine the dominant PNV of each

ecosection, based on soil drainage, landform/soil type, and sometimes ecodistrict. These decision keys are shown for two Acadian ecoregions in Fig. 5a-b and two Maritime Boreal ecoregions in Fig. 5c-d. PNV decision keys for the remaining ecoregions are included in Figure A1, along with notes specific to ecosection interpretation (see supplementary material). Note that the columns soil drainage and landform/soils in Fig. 5 and Figure A1 were used to define ecosection, directly from the Nova Scotia ecological land classification system (Neily et al. 2017). The dominant PNV was then assigned to each ecosection based on NSDLF staff expert knowledge of species occurrence as a function of drainage, landform, and soils within each ecosection. Non-forest communities such as open wetlands, barrens, rocklands, coastal beaches, salt marshes and dykeland were combined and mapped as “Other”. It is important to note that our basic unit for assigning a PNV was the ecosection, which can be a large area and therefore have inclusions of differing forest conditions.

4.4 Assigning natural disturbance regimes to PNV forest communities

After determining PNV, the second step of our process (Fig. 1) involved assigning hurricanes, spruce budworm, windstorm, and fire natural disturbance regimes defined by Taylor et al. (2020) to each PNV. This considered species composition, location, spatial distribution of disturbances, and susceptibility to each disturbance agent (Taylor et al. 2020). Data sources, analyses, and assumptions for each of the four major disturbance agents in Nova Scotia are described below. For each disturbance agent, we begin by reiterating the Taylor et al. (2020) categorization of spatial extent, severity, return interval, and MADR, done at the provincial or ecoregion scale, and then, if possible, extend that to the finer scale PNV forest community level. Overall, rates (% area yr⁻¹) of high, moderate, and low severity disturbances in each PNV were calculated by summing rates for individual disturbance agents.

4.4.1 Hurricanes

Hurricane disturbances in Nova Scotia are consistently wide scale (>500ha) with long-term (>150 years) return intervals but the severity of each hurricane event varies across the landscape (Taylor et al. 2020). Based on data from surveys following Hurricane Juan, a major Category 2 hurricane that damaged a wide forest area across central Nova Scotia in 2003 (and is the only Nova Scotia hurricane followed by detailed intensive forest damage surveys and analyses), Taylor et al. (2020) determined the return interval and MADR for each severity level for all of Nova Scotia. High-severity windthrow had a return interval of 1250 years (0.08% yr⁻¹), moderate severity was 714 years (0.14% yr⁻¹), and low severity was 1111 years (0.09% yr⁻¹). However, low-severity windthrow from hurricanes is likely underestimated (Taylor et al. 2020). We reanalyzed the Hurricane Juan damage survey data by assessing a random sample of 250,000 points across the affected landscape to calculate proportions of low (<30%), moderate (30-60%), and high (>60%) severity windthrow in each of five broad stand cover types.

This showed a higher proportion of high severity windthrow area for Softwood and Spruce-balsam fir (35-36%) stand types than for Hardwood, Mixedwood, or Pine stands (25%, 27%, and 29%, respectively). We therefore applied the resulting proportions of low, moderate, and high severity area for three PNV groupings: 1) Tolerant Hardwood, Floodplain, and Maritime Boreal Coastal Hardwood; 2) Tolerant Mixedwood and Tolerant Softwood; and 3) Coastal Spruce-Fir, Highland Fir, Spruce-Pine, and Acadian and Maritime Boreal Wet Coniferous. Because these MADR data are based on only a single hurricane, similar data should be collected from other hurricanes in the future, so extrapolations can be more robust than from a single episode.

4.4.2 Spruce budworm outbreaks

Spruce budworm disturbances in Nova Scotia are consistently wide-scale (>500ha) with short term return intervals (<50 years, usually 30-40 years) (Taylor et al. 2020). Spruce budworm outbreak severity (% tree mortality) varies with host species: balsam fir >60%; white spruce and red spruce 30-60%; and black spruce <30%. Assuming a 40-year return interval and prorating area disturbed by host species mortality rate (balsam fir 85%; white, red, and black spruce 60%, 40%, and 20%, respectively), MADRs would be 2.1% yr⁻¹ for balsam fir, 1.5% yr⁻¹ for white spruce, 1.0% yr⁻¹ for red spruce, and 0.5% yr⁻¹ for black spruce. Balsam fir abundance is highest in the Cape Breton Highlands, Nova Scotia Uplands, Northern Plateau, and Northumberland/Bras D'Or ecoregions and lower in the Western, Valley and Central Lowlands ecoregion (Taylor et al. 2020). Spruce budworm outbreak occurrence and severity vary depending on location in Nova Scotia (Taylor et al. 2020): every 30–40 years and moderate to severe in Cumberland, Colchester, Pictou, Antigonish, Inverness, and Victoria counties; every 30–40 years and low to moderate severity in Annapolis, Kings, Hants, Guysborough, Richmond, and Cape Breton counties; and very low or no outbreaks in Digby, Yarmouth, Shelburne, Lunenburg, and Halifax counties. Therefore, on mainland Nova Scotia, where red spruce mainly occurs, budworm outbreaks severe enough to cause mortality mainly occur in the northern half of the province, so we reduced the red spruce mortality rate from 1.0% to 0.4%. Spruce budworm only defoliate balsam fir and spruce and do not influence hardwood or pine forests, resulting in partial disturbances of mixedwoods. Therefore, depending upon overall mortality, spruce budworm outbreaks were categorized as either moderate or high severity.

4.4.3 Windstorm

Spatial extent of windstorms in Nova Scotia is typically medium (50-500ha) or wide scale (>500ha) (Taylor et al. 2020). Return intervals for high- and moderate-severity windthrow averaged 5000 years (0.02% yr⁻¹) (Taylor et al. 2020), based on data from the NSDLF PSP database. Low severity windthrow, with 5-30% mortality, had a return interval of only 71 years (1.4% yr⁻¹) (Taylor et al. 2020).

To determine windstorm severity by PNV for the current paper, we reanalyzed windthrow data from 2008-2017 (post-Hurricane Juan) in 2,800 5-yr re-measurements of PSPs (400 m²) randomly located across Nova Scotia forests. Only plots that contained at least 10 living trees (stems > 9.0 cm DBH) were included to avoid sampling very young, regenerating stands. Windthrow for each plot was calculated by tallying the number of downed trees (with stem elevation angle <45°) and stem-broken trees since the last measurement and calculating the proportion of basal area impacted. This proportion was divided by the number of years since the last measurement, to derive the mean annual windthrow disturbance rate per plot, and plot estimates were averaged by PNV forest community. However, because PSPs were only measured every 5 years, it is probable that higher severity wind damage occurrence was underestimated by dividing by the 5-year period. Therefore, we also calculated cumulative 5-yr windstorm rates based on the same plot data, to identify probable moderate and high severity windthrow events caused by windstorms.

4.4.4 Fire

Natural fire (i.e., lightning-caused, with no fire suppression) spatial extent was estimated to be wide scale (>500ha) and long-term (> 150 years return interval) (Taylor et al. 2020). However, fire rates vary by species, ecoregion, and ecosite (Taylor et al. 2020). Fire spatial extent for both human-caused and lightning ignitions was largest in the Western, Northumberland Bras D'Or, and Eastern ecoregions; intermediate in the Atlantic Coastal and Valley and Central Lowlands ecoregions; and smallest in the Northern Plateau, Cape Breton Highlands, Nova Scotia Uplands, and Fundy Shore ecoregions. Fire severity was usually either high (>60% of stand killed) or moderate (30–60% of stand killed). Ponomarenko (2018) determined past fire occurrence ages based on analysis of charcoal sediments in depressions from uprooted trees that act as local sediment traps. Fire return intervals varied from 250–600 years depending on species and ecosite: black spruce—pine, 250–300 years; Acadian tolerant softwood, 500 years; Acadian tolerant hardwood, 500 years; and wet coniferous, 600 years (Ponomarenko 2018). To refine fire return interval data for the current paper, we examined the Ponomarenko (2018) fire history data from 15 locations across Nova Scotia, representing four PNVs, and calculated fire return interval at the site and PNV scale.

Estimating the occurrence of forest fires without fire suppression is problematic because fire suppression has been pervasive and highly successful in Nova Scotia. Number of fires per year has averaged 220 to 450 over the last four decades, but these burned <2000-3000 ha yr⁻¹ (Taylor et al. 2020). In contrast, large historical fires were recorded, e.g. by Simeon Perkins (1766–1812), who described a fire south of Lake Rossignol in 1800 that covered an estimated 175 000 ha (Champlain Society 1948), and Titus Smith (1802), in Queens and Lunenburg counties, where an estimated 150 000

ha burned in 1720 (Hawboldt 1955). Therefore we undertook additional modelling analyses to explore the potential impact of fire in Nova Scotia.

The natural cause of forest fire ignition in Nova Scotia is lightning strikes. Since 1990, origins of fires (based on area burned) was 1% lightning, 90% human (37% incendiary, 40% recreation or residents, 11% industry or railways), and 9% unknown (Taylor et al. 2020). However, human-caused fire suppression confounds our ability to estimate actual, natural fire regime parameters and these 20th century data are not indicative of what would occur naturally. Reflecting effective fire suppression, most of the 260 lightning-caused fires since 1970 were ≤ 2 ha, while the remainder ranged from 2.1–17 ha. The seven largest lightning-caused fires were 163 ha in 1929, 100 ha in 1930, 370 ha in 1942, 283 ha in 1944, 192 ha in 1952, 517 ha in 1961, and 113 ha in 1965 (Taylor et al. 2020).

We used lightning strike data (Fig. 6) and fire spread modelling using the BURN-P3 model (Parisien et al. 2005), which has been calibrated to simulate forest fire behavior in Nova Scotia, to project spread of lightning-caused fires in current Nova Scotia forests if there were no fire suppression. Lightning occurs throughout Nova Scotia at about 0.2–0.3 flash $\text{km}^{-2} \text{yr}^{-1}$, with a few areas reaching 0.35–0.4 flash $\text{km}^{-2} \text{yr}^{-1}$ (Fig. 6a). The average amount of lightning for Nova Scotia from 1999–2018 was approximately 24,600 strokes per year, while 2007 and 2011 had high lightning occurrence (77,600 and 67,000 strokes yr^{-1}). Thus, there is considerable potential for fire starts coinciding with high severity fire conditions. From 1959 to 2019, a total of 360 lightning-caused fires occurred in Nova Scotia (Taylor et al. 2020). The Western ecoregion was highest at 10.1 lightning-caused fires per 1000 km^2 (Fig. 6b), Northern Plateau and Atlantic Coastal were lowest at 0.0 and 2.1, and all other ecoregions had from 4.3–6.5 lightning-caused fires per 1000 km^2 from 1959–2019 (Taylor et al. 2020). The question becomes “over long periods (i.e., centuries), how large might these lightning fires get if there was no human-caused fire suppression?” Large fires invariably result from coincidence of ignition sources with high severity Fire Weather Index (FWI) conditions.

Unsuppressed lightning-ignited fires were simulated based on 3,000 iterations with three fires per iteration (9000 fires) using BURN-P3 (Parisien et al. 2005) and retaining only fires greater than 200 ha (Wang et al. 2014). Model inputs included spatial layers (100 m resolution raster grids) for forest fuels, topography, and relative probability of lightning ignitions, and environmental variables including season, fire duration, number of hours of burning per day, daily fire weather conditions, and number of fires per iteration. These variables and assumptions are described in Table S1. The ignition grid for the model was based on historic lightning fires from fire reports. Burn probability was calculated as number of times a pixel burned divided by the number of iterations, multiplied by 100. We recognize that climate change will affect fire severity and perhaps lightning fire occurrence, but the topic is beyond the

scope of this paper, and regardless, would still be modified by fire suppression.

BURN-P3 simulation results indicated that fire was most probable in the Spruce-Pine (nearly 3,200 out of 9,000 fires) and Tolerant Softwood (2,300 fires) PNVs (Table 4). Mean simulated unsuppressed fire size was 2,200-2,900 ha in the Spruce-Pine, Acadian and Maritime Boreal Wet Coniferous, and Highland Fir PNVs, and 1,400-1,900 ha in all other PNVs. Maximum simulated fire size was 14,600-15,400 ha in the Spruce-Pine and Tolerant Softwood PNVs and 4,400-11,900 ha in other PNVs (Table 4). Fire suppression will not end, but these results suggest that fire disturbance regimes are undoubtedly more dominant in Nova Scotia than indicated by 20th and 21st century fire occurrence, especially in the Spruce-Pine PNV and Western ecoregion. Lightning ignition values, burn probability, and total area burned map simulation results are included in Figure A2.

4.5 Pooled multi-rotation model calculations

For each PNV, disturbance-agent-specific MADRs were pooled by severity level (high, moderate, or low). These provided the “target” MADR data needed to create and solve pooled multi-rotation models (as described in Section 2.3.2 and Fig. 2) for each PNV severity level. Pooled multi-rotation models were based on partitioning the PNV landscape into three land area allocations (described by percentage) to represent short, medium, and long rotation lengths (or entry times for moderate-to-low intensity partial-cutting) to represent the distribution of TSD unique to each PNV. We use three land area allocations here for demonstration purposes, but in practice, the landscape could be partitioned into as many land area allocations as desired for different management situations. Percent land area allocations and MADR for each rotation length or entry time were determined by an iterative method that repeatedly fitted different combinations of percent area allocations and MADR until an optimal solution was achieved that met four primary constraints: 1) sum of the area-weighted MADRs had to equal the overall PNV target MADR; 2) percent land area allocations had to sum to unity (i.e., 100%); 3) resulting “grey rectangles” (as defined in Fig. 2c) had to generally approximate the natural TSD distribution as described by the negative exponential curves for each PNV; and 4) rotation lengths and entry times had to make practical sense considering operational constraints and tree species silvics (e.g., tree longevity and optimal merchantable age). For example, rotations approximating high-severity disturbances had to be long enough to allow merchantable wood to form, yet short enough, in some cases, to not pass optimal tree longevity for merchantability, as the case for balsam fir dominated PNVs. Optimal solutions were derived for each pooled multi-rotation model using both a customized optimization algorithm written and executed in the R statistical software environment (R Core Team, 2021) and expert opinion of the authors.

All maps, with the exception of Fig. 6, were created with data from the Nova Scotia Department of Lands and Forestry using ArcMap v. 10.5.1 and ArcGIS Pro v. 2.5 with the North American Datum of 1983 (NAD83) and Universal Transverse Mercator (UTM) projection and coordinate system. The maps in Fig. 6 were generated by Environment and Climate Change Canada's Canadian Lightning Detection Network.

5. Findings

5.1 PNV mapping results

Mapped locations of each zonal and azonal PNV forest community are shown in Fig. 7. The most prevalent PNVs were Tolerant Hardwood (22.8% of the province's 5.5 million ha area), Tolerant Softwood (20.5%), and Spruce-Pine (26.9%) (Table 3). Other PNVs, in order of occurrence, were Tolerant Mixedwood 7.4%, Coastal Spruce-Fir 5.5%, Acadian and Maritime Boreal Wet Coniferous 4.1%, Highland Fir 2.9%, Floodplain 0.6%, and Coastal Hardwood 0.4% (Table 3).

The distribution of PNVs by Ecoregion is summarized in Table 5. Tolerant Hardwoods dominated (>50% of area) in the Nova Scotia Uplands (Ecoregion 300) and Fundy Shore (900) ecoregions, while Highland Fir dominated (73%) in Cape Breton Highlands (200) and Coastal Spruce-Fir (65%) in the Atlantic Coastal (800) ecoregions (Table 5). There was a substantial amount (16-48%) of azonal Spruce-Pine PNV in most Acadian ecoregions (300-700, but 900 was lower) (Table 5).

Fig. 8 more clearly shows the relative dominance of PNVs in different areas of the province. Tolerant Softwood (primarily red spruce and hemlock) was prevalent throughout much of mainland Nova Scotia (Fig. 8c), while Highland Fir was restricted to the Cape Breton Highlands (Fig. 8d). Tolerant Hardwood was prevalent in most of Nova Scotia except the southwest portion (Fig. 8a), which had more Spruce-Pine (Fig. 8f). Coastal Hardwood and Coastal Spruce-Fir PNVs were restricted to the southern coastal region (Fig. 8e) and Tolerant Mixedwood primarily to central Nova Scotia (Fig. 8b).

The PNV distribution provides a target stand type or species composition and also helps to define appropriate landscape and stand-level management actions. However, current forest species composition is also important, in determining appropriate treatments to reach the PNV-based target – i.e., “How do we get there from here?” given current and target compositions. Fig. 9 illustrates the current distribution of 10 major tree species in Nova Scotia, in 10% crown cover classes. Sugar maple, yellow birch, and red spruce (Fig. 9a, b, e) are typical long-lived Acadian Forest species, which, depending on their proportions, result in Tolerant Hardwood, Tolerant Mixedwood, or Tolerant Softwood PNVs. Balsam fir high cover (Fig. 9h) coincides well with the Highland Fir PNV. White pine (Fig. 9i) and red oak (Fig. 9d) are most prevalent in southwestern Nova Scotia.

Table 6 helps to assess “How far we have to go” in achieving PNV species composition, by summarizing percentage area of the top 12 current species, which comprise 95% of species cover of Nova Scotia forests, by PNV community. Bold font values in Table 6 are generally considered late successional species within a given PNV. For example, the Tolerant Hardwood PNV area currently has 12.7% sugar maple 11.0% yellow birch and 16% red maple, which are appropriate, but also 11% white spruce, 15% balsam fir, and 8% white birch, which are not typical of the Tolerant Hardwood PNV. Tolerant Mixedwood and Tolerant Softwood PNV areas also contain large amounts of species that do not fit well in those PNVs, though a certain proportion of early-to-mid successional species/communities will always be present even in the absence of human disturbance, as a result of natural disturbances. Further research on the natural range of variability is needed to quantify those proportions. In contrast, the Coastal Spruce-Fir, Highland Fir, Spruce-Pine, and Acadian and Maritime Boreal Wet Coniferous PNV areas have current species composition more in line with the PNV targets. The current Nova Scotia forest has large areas (over 500,000 ha each) of red maple, black spruce, and balsam fir (Table 6). While a certain proportion of the landscape will always be in an early- and mid-successional state, given the presence of natural disturbances, it is clear that there is currently an over-representation of early-mid successional stands and species such as balsam fir and red maple in some PNVs, due to human influences.

5.2 Natural disturbance regimes by PNV

Fire return intervals derived from the reanalyzed carbon sediment dating data (Ponomarenko 2018) ranged from 521-595 years for Tolerant Hardwood, 294-354 years for Tolerant Softwood, and 172-220 years for Spruce-Pine (Table S2). Generalizing these data in combination with values from Taylor et al. (2020), we defined fire return intervals and disturbance rates in four classes: 500 years and 0.20% yr⁻¹ for Tolerant Hardwood, Tolerant Mixedwood, Floodplain, and Coastal Hardwood PNVs; 300 years and 0.33% yr⁻¹ in Tolerant Softwood, and in the absence of other data (but see section 4.4.4 about fire disturbance) we assumed this also applied to Highland Fir and Coastal Spruce-Fir; 200 years and 0.5% yr⁻¹ for Spruce-Pine in the Acadian PNV; and 600 years and 0.17% yr⁻¹ for black spruce in the Acadian and Maritime Boreal Wet Coniferous PNVs (Table 7).

Windstorm disturbance results based upon reanalysis of the PSPs from 2008-2017 (see Table A2) was <0.001% yr⁻¹ for both high and moderate severity windthrow, but low severity windstorm disturbance varied among PNVs from 0.00-7.7% yr⁻¹ (Table 7). In this analysis, we divided low severity disturbance further into <5% and 5-30% yr⁻¹ mortality, because of the high prevalence (92-100% of cases) of very low <5% yr⁻¹ windthrow (Table A2). Even within the <5% and 5-30% yr⁻¹ classes, median

windthrow was much lower than the class midpoints, at 0.29-0.84% yr⁻¹ and 6.2-13.0% yr⁻¹, respectively (Table A2), indicating the ubiquitous nature of very low severity windthrow. Since PSPs were only measured every 5 years, dividing the cumulative windthrow by 5 to calculate annual values may underestimate more severe windthrow. Therefore, we also calculated moderate severity (30-60% yr⁻¹) windthrow, assuming it occurred in single events (Table A2). No moderate severity windthrow occurred in Floodplain and Maritime Boreal Wet Coniferous PNVs, but there was 0.22-0.49% yr⁻¹ in six PNVs, and it was highest at 1.28-1.54% yr⁻¹ in the Coastal Hardwood and Coastal Spruce-Fir PNVs (Table A2).

Hurricane damage varied among PNVs in terms of the distribution of low, moderate, and high severity disturbance, with a higher proportion of high severity windthrow area for softwood and spruce-balsam fir (35-36%) stand types than for hardwood, mixedwood, or pine stand types (25%, 27%, and 29%, respectively) (Table 7).

Spruce budworm outbreaks had the highest annual disturbance rate at 2.1 % yr⁻¹ for Highland Fir, 1.5% yr⁻¹ for Coastal Spruce-Fir, 0.5% yr⁻¹ for Tolerant Mixedwood, Spruce-Pine, and Acadian and Maritime Boreal Wet Coniferous, and 0.4% yr⁻¹ for Tolerant Softwood (Table 7). It is important to note that windstorm, fire, and hurricane disturbances affect all species in a stand, but spruce budworm only affects (defoliates and kills) the host balsam fir-spruce species, and may actually increase growth rates of residual surviving non-host trees (Hennigar et al. 2007).

The primary disturbance agents were spruce budworm in Highland Fir and Coastal Spruce-Fir PNVs and fire in the Spruce-Pine and Acadian and Maritime Boreal Wet Coniferous PNVs. Overall summed severe disturbance rates of all four disturbance agents divided PNVs into six classes with increasing disturbance rate and decreasing return interval (Table 8). The Tolerant Hardwood, Floodplain, and Coastal Hardwood PNVs had the lowest high severity disturbance rate of 0.28% yr⁻¹ and a return interval of 357 years. Total high severity disturbance rates increased to 0.53% yr⁻¹ for Tolerant Mixedwood, 0.61% yr⁻¹ for Tolerant Softwood, 0.75% yr⁻¹ for Spruce-Pine and Wet Coniferous, 1.16% yr⁻¹ for Coastal Spruce-Fir, and was highest at 2.1% yr⁻¹ for Highland Fir (Table 8). These rates equated to disturbance return intervals of 189, 164, 133, 86, and 48 years, respectively (Table 8). Generally, the hardwood PNVs had fewer high-severity disturbances, resulting in stand dynamics dominated by individual or small group tree deaths and gap processes. Spruce budworm was the dominant disturbance wherever its host species occur, with the exception of the most southerly part of Nova Scotia where budworm outbreaks do not occur (Taylor et al. 2020).

MADR and return intervals for moderate and low severity disturbances are summarized by PNV in Table 8. The Coastal Hardwood and Coastal Spruce-Fir PNVs had the highest rate of moderate severity disturbances, at 1.68-2.17% yr⁻¹, or return intervals of 46-60 years (Table 8). Floodplain PNV forest

communities had the lowest moderate and low severity disturbances, at 0.14 and 0.09% yr⁻¹ (return intervals 714-1111 years). Other PNVs had moderate severity disturbances ranging from 0.34-0.88% yr⁻¹ (return intervals of 114-294 years) (Table 8). Low severity disturbances, driven mainly by windstorms, ranged from 1.19-7.79% yr⁻¹, or 13-84 year return interval, except for very low rates for Floodplain and Maritime Boreal Wet Coniferous PNVs, where few PSPs were present (Table 8).

Return intervals and MADR were used to infer target TSD distributions similar to the example in Fig. 2c, for high severity disturbances (Fig. 10) and low and moderate disturbances (Table 10). For example, for the Tolerant Hardwood, Floodplain, and Coastal Hardwood PNVs with the lowest MADR of 0.28% yr⁻¹ and longest 357-year return interval, based on few high severity disturbances (Table 9), rotation lengths would be 200 years for 35% of the forest, 500 years for 40% of the area, and 1000 years for 25% of the area (Fig. 10a). It is important to note that the rotation lengths and entry times proposed here for forest management are equivalent to TSD (years since last disturbance) and not species longevity. In contrast, in the Highland Fir PNV with the highest MADR of 2.1% yr⁻¹ and 48-year return interval, from frequent stand-replacing spruce budworm outbreaks, rotation lengths would be 35 years for 50% of the area, 60 years for 30% of the area, and 120 years for 20% of the area (Fig. 10f). These are consistent with the 87% mean balsam fir mortality measured in 30 stands in the Highland Fir PNV in the 1970s-1980s spruce budworm outbreak (MacLean and Ostaff 1989). As MADR for high severity disturbances increased from 0.53% yr⁻¹ to 1.16% yr⁻¹ in the remaining PNVs (Fig. 10b-e), 40-50% of the PNV area was assigned to the shortest class (top grey boxes in Fig. 10) with rotation lengths of 60-125 years, while the remaining 50-60% of area per PNV had rotation lengths ranging from 120-500 years (Fig. 10b-e).

The MADRs and proposed rotation lengths by PNV in Fig. 10 are based solely on high severity disturbances, but nearly all disturbances also result in substantial areas of moderate and low severity disturbance (Tables 7, 8). MADRs and return intervals for moderate and low severity disturbances by PNV are summarized in Table 10. In contrast to high severity disturbances that result in >60% mortality and can be approximated by high intensity, stand-replacing harvesting practices (e.g., clearcutting), moderate and low severity disturbances would be approximated by partial or variable retention harvests (e.g., partial harvesting methods), so we report entry times (Table 10). Different intensities of harvesting would have to be used to emulate high, moderate, and low severity disturbances. The length of the grey boxes (rotation length or entry time) is a proxy for return interval, representing the time it would take for the entire area to be disturbed by that severity of disturbance (or intensity of harvest method) at the given MADR. As an example, moderate severity disturbances in the Tolerant Hardwood PNV would result in 55%, 25%, and 20% of the area managed under 150 yr, 300 yr, and 600 yr entry

times, respectively, while low severity disturbances would be approximated by 40%, 35%, and 25% of the area managed under 25 yr, 50 yr, and 125 yr entry times (Table 10). Apart from the Floodplain and Maritime Boreal Wet Coniferous PNVs with extremely long (500-3000 yr) return intervals based on limited data (few PSPs available within these PNVs), return intervals for moderate severity disturbances in other PNVs ranged from 35-180 yrs for the most frequent and from 140-900 yrs for the least frequent return intervals (Table 10). Similar ranges of return intervals for low severity disturbances were 10-60 yrs and 30-240 yrs (Table 10). We view the area distributions in Fig. 10 and Table 10 as a guide for purposefully selecting area distributions and TSD intervals that are appropriate for ecological forestry goals. In many cases, there are not adequate data to define the distributions of disturbance severities, nor the degree of spatial overlap of major disturbance agents. Thus our target MADRs, rotation lengths and entry times are primarily a guide for selecting a management regime that meets ecological forestry objectives that are both established in the literature and adopted by Nova Scotia. These MADRs and corresponding rotation lengths and entry times by PNV should be the basis for silviculture prescriptions developed to manage forests in Nova Scotia. We believe that the graphs in Fig. 10 show an accurate longevity of climax species by PNV and that we could support those ages with reference stand ages of the very limited areas of old growth forests that are available. But this would be difficult from a natural forest area of sufficient size, due to the long harvesting history and high percentage of private land ownership in Nova Scotia compared to other forested regions of Canada.

In addition to landscape-level effects of disturbance regimes, stand-level measures are also affected. Stand-level age-class distribution would be all-aged for Tolerant Hardwood, Floodplain, Coastal Hardwood, Tolerant Mixedwood, and Tolerant Softwood PNVs; multi-aged (with some trees surviving disturbance) for Spruce-Pine, Wet Coniferous, and Coastal Spruce-Fir; and single-aged with retention (a small 2nd cohort) for Highland Fir (Table 9). The distribution of severity of disturbances by PNV generally indicates the amount of tree structure left after natural disturbances, which can help prescribe retention rates. The % of area killed in three mortality classes reflects the mean biomass killed (Table 9). So Tolerant Hardwood, Floodplain, Coastal Hardwood, and Mixedwood PNVs always had low (<30%) mortality; Tolerant Softwood had a mix of low and moderate (30-60%) mortality; and Spruce-Pine, Wet Coniferous, Coastal Spruce-Fir, and Highland Fir PNVs all had a mix of moderate and high (>60%) mortality rates. These distributions of mortality rates should be a primary factor in determining area of high, moderate, and low severity harvesting and corresponding rotation lengths and entry times. Future research should better define distribution of mortality as a function of disturbance severity and stand and site conditions.

6. Discussion

Ecological forestry provide a comprehensive ecosystem-based framework for managing forests for human needs, while also maintaining forest health under a changing environment (Kuuluvainen et al. 2021). Ecological forestry aims to maintain substantial wood production while minimizing reductions in biodiversity, and includes both landscape-level and stand-level considerations. At the landscape level, ecological forestry requires careful design of harvest blocks and resulting stand configuration (size, shape), age-class distributions, harvest rotation lengths, and entry times based on TSD for each PNV. Stand-level treatments must also be designed for specific PNVs to create and maintain appropriate vertical diversity in the forest canopy and ensure that biota present in ecologically mature and old-growth forests occur in regenerating stands (Seymour and Hunter 1992). Stand-level prescriptions must also leave an appropriate number and arrangement of large living trees and standing dead snags, and adequate levels of large downed dead woody material during the regeneration phase (Seymour and Hunter 1992). Ecological forestry should also include monitoring of effectiveness, by measuring response of sensitive biodiversity metrics to landscape- and stand-level harvest prescriptions and appropriately acting upon the findings.

Although many of the PNV forest communities in Nova Scotia periodically have high severity wind, fire, or insect disturbances, some PNVs have few severe disturbances and thus are largely renewed via single tree or small group tree mortality and gap dynamics. These include Tolerant Hardwood, Floodplain, Coastal Hardwood, Tolerant Mixedwood, and to an extent, Tolerant Softwood PNVs. In these types, local stand and site features combined with broader scale climatic and physiographic gradients determine gap occurrence and heterogeneity, which is driven by moderate and low severity disturbances. Disturbance patterns within forest regions can be markedly variable, even across similar soil and stand conditions (e.g., Lorimer and White 2003; Messier et al. 2005; Després et al. 2017).

Gap causing disturbances are considered a characteristic driver of stand dynamics of many forest types in the Acadian Forest Region (e.g., Seymour et al. 2002; Lorimer and White 2003; Baldwin et al. 2019a, Basquill and Baldwin 2020). Lightning fire ignitions and stand-replacing fires in general are less common in the Acadian Forest than in other areas of Canada (Boulanger et al. 2014; White et al. 2017; Basquill and Baldwin 2020). Historical records such as early land survey reports and associated witness tree data suggest a preponderance of late seral tree species and stand conditions (e.g., Lorimer 1977; Lutz 1997; Blackadar 2002; Loo and Ives 2003; Aube 2008). Life history traits of tree species characterizing zonal sites in the Acadian Forest, most of which are long-lived, shade-tolerant, and slow-growing, are characteristic of biomes with uncommon catastrophic disturbance (Jactel et al. 2017), and

are adapted to gap-scale disturbance regimes (Canham 1989; Attiwill 1994). Mean gap size in the Acadian Forest and similar northeastern forests ranges from 24-126 m², within an overall average of 53 m² (Seymour et al. 2002). Little research has been conducted on gap dynamics in Nova Scotia, which is required to provide baselines for devising effective ecological forestry practices across natural ranges of variation. New research is required to fill this void, as well as better understanding of frequency and effects of low and moderate severity disturbances in Nova Scotia.

An important point about ecological forestry is that disturbances such as windstorms and hurricanes will continue to occur, regardless of forest management and prevention activities, so care must be taken that they not be 'double counted'. Fire differs in some respects, because it occurred historically in Nova Scotia but no longer does to the same extent because of fire suppression. Fire suppression has clearly reduced the extent and severity of lightning-caused fires that occur under severe fire weather conditions. Simulations of potential fire spread under no-suppression and current weather conditions indicated that large fires were relatively infrequent, but maximum fire size could be >10,000ha in four PNVs (Spruce-Pine, Tolerant Softwood, Acadian Wet Coniferous, and somewhat surprisingly, Tolerant Hardwood), and 4,400-9,400ha in remaining PNVs. Simulated fire was especially prevalent in some azonal PNVs in Nova Scotia.

Past human activities (especially land clearing and forest harvesting) have altered landscape age structure and tree species composition, which in turn, influence natural disturbance patterns, current biodiversity, and ecosystem resilience. Harvesting has been the dominant disturbance agent in forests of the northeastern United States (Brown et al. 2018) and in Nova Scotia (Cheng and Lee 2009; Colville and Prakash 2010), driving declines in biodiversity and ecosystem services (Miller and McGill 2019). Spruce budworm outbreaks may occur regardless of management unless Nova Scotia acts to mitigate outbreak effects by spraying insecticides to prevent mortality or outbreaks (MacLean 2016; MacLean et al. 2019). If the Nova Scotia public desires to return its forests to a more natural condition through implementation of ecological forestry, this might require reducing harvest levels so as to not 'double count' and account for future natural disturbances. Furthermore, harvest reduction and increased retention may be required to promote recovery of biodiversity and ecosystem services lost through past harvest and land clearing pressures (Fedrowitz et al. 2014; Mori et al. 2017). However, potential sustainable harvest in Nova Scotia is ~5.7 million m³ yr⁻¹ (Canadian Council of Forest Ministers 2020), considerably higher than the current annual harvest of ~3.3 million m³ yr⁻¹ (NSDLF 2020), although harvest levels vary based on standing stock levels, market conditions, and private landowner decisions. Implementation of ecological forestry should consider if natural disturbances are likely to be additive to management disturbances and how protected areas and high-production plantations contribute to the

total annual disturbance in the province. Given that many if not all disturbances will occur in protected areas, they must be included in landscape (PNV) level accounting of natural and management disturbances.

For some natural disturbances, forest management can be used to reduce disturbance risk and vulnerability. Altering tree species and age classes can reduce vulnerability to insect damage (e.g., MacLean 1996); altering softwood/hardwood composition is one means towards “fire-proofing” forest (e.g. Hirsch et al. 2001); and managing forest edges and opening sizes can reduce susceptibility to windthrow. Also, ecological forestry should consider forest succession and species composition as guidance in addition to the amount of area disturbed. One of the main benefits of ecological forestry is retention or potentially restoration of biodiversity and ecosystem integrity. But metrics and quantitative targets for biodiversity and ecosystem integrity need to be proposed and monitored as an integral part of ecological forestry; these biodiversity targets are lacking in Nova Scotia, highlighting a critical information gap.

A key challenge that faces forests and forestry, in addition to implementation of ecological forestry, is climate change. The frequency and severity of many natural disturbances is increasing (Dale et al. 2001; Seidl et al. 2017), which poses challenges for basing management decisions on historical natural disturbance parameters that are shaped by historical climate patterns. An important unknown is how climate change is expected to alter each of the key disturbance regimes in this analysis. A higher frequency of extreme storm and drought events is generally expected to increase the severity of fire, hurricane, and wind events (Knutson et al. 2010; Boulanger et al. 2014; NOAA 2019). Warming temperatures and more frequent severe drought and extreme heat events are predicted to lead to increased wildfire disturbance in Nova Scotia, with longer fire seasons and increases in annual area burned (Boulanger et al. 2014). However, fire suppression has greatly reduced these impacts in recent decades (Taylor et al. 2020) and climate change may have as much, or more, budgetary impacts on fire or insect protection than ecological impacts on the landscape. The effects of climate change on windstorms is highly uncertain due to their smaller scale and representation in global circulation models (Peterson 2000). However, increasing amounts of convection in the atmosphere due to climate warming and rising sea temperatures are expected to lead to more frequent and/or severe windstorms and hurricanes (Taylor et al. 2020).

Climate change effects on forest insect disturbances will also be highly variable and complex, depending on the life cycle and phenology of a given species and climatic impacts on host tree species. Climate warming is expected to decrease spruce budworm outbreak duration and severity due to adverse impacts on the budworm life cycle (Gray 2013), but it is also predicted that increasing synchrony

between budworm larval emergence and budburst of the secondary host species black spruce could increase defoliation and mortality (Pureswaran et al. 2015). Black spruce is the second most abundant tree species by percent cover in Nova Scotia, after red maple. Potential changes in tree species distribution and forest composition with the warming climate – especially in transitional zones like the Acadian Forest Region (Steenberg et al. 2011; Taylor et al. 2017b) – add further complexity due to potential changes in vulnerability to different disturbances. For example, a decline in some colder-climate boreal species like balsam fir could reduce the importance of spruce budworm as a disturbance agent in the future over the long term, but trees stressed by climate anomalies over the short term may sustain higher mortality rates from a given amount of defoliation.

Warming conditions combined with trade-connected economies are also leading to more introduced invasive pests like the hemlock woolly adelgid (*Adelges tsugae*) and the beech leaf-mining weevil (*Orchestes fagi*) (Taylor et al. 2020). Eastern hemlock and American beech are ecologically important tree species in Acadian forests and are experiencing high rates of mortality without available effective control measures. While long-term management options are being investigated for the hemlock woolly adelgid, the beech leaf-mining weevil is not even regulated and there are no known emerging management options. While uncertainty levels remain high regarding the severity and impacts of climatic change, it is clear that no single management framework will be sufficient, and that multi-faceted approaches that enhance ecosystem resilience are needed (D'Amato and Palik 2021).

Another challenge specific to Nova Scotia and some other regions is the disparate pattern of land ownership, with only about 1.5 million ha, or 29% of the province, being Crown lands under the administration and control of the provincial government. Having 70% of the forest area owned by thousands of owners complicates any implementation of ecological forestry and PNV guidance for forest management, although with PNVs mapped for the whole province, guidance can be provided for all ownerships. Finally, a limitation to this study, and a challenge to application of this work elsewhere, is the detailed input data required to create PNVs and identify their appropriate disturbance regime. Assigning PNVs was dependent upon the detailed ecological land classification in Nova Scotia (Neily et al. 2017) and the soil drainage and landform information used to map ecosection (Table A1), and identification of natural disturbance regimes by PNV was dependent on the analysis of disturbances conducted by Taylor et al. (2020). Ideally, disturbance regime characterization includes sufficient data to reflect the natural range of variation (Landres et al. 1999; Cyr et al. 2009).

We used three classes and thresholds to describe the spatial extent, severity, and return interval of natural disturbances that were tailored to address the unique disturbance ecology and forest management culture of Nova Scotia. These are generally similar to the range of values and class systems

used elsewhere to describe disturbance regimes (e.g., Bergeron et al. 2002; Seymour et al. 2002; Roberts 2007; Lafleur et al. 2018). Even if other disturbance classes are more appropriate in other regions, the PNV multi-rotation model framework is still applicable, as long as a robust ecological land classification system and some knowledge of the natural disturbance regime are available. However, our use of the negative exponential function to approximate landscape age-class distribution may be less appropriate in forest ecosystems where the dominant natural disturbance(s) are distinctly non-random in their occurrence, as if the dominant disturbance only affects certain tree species or age cohorts. In such situations, other approximations of landscape age-class distribution may be required—but the multi-rotation model method should still be applicable.

The motivation behind this analysis was to help develop management guidelines for ecological forestry in Nova Scotia, specifically by defining natural disturbance regimes for ecological forestry. For the major disturbance agents fire, hurricanes, windstorm, and spruce budworm outbreaks, we calculated return intervals and MADRs and corresponding harvest rotation lengths or entry times for each PNV forest community. Using ecosection from the Nova Scotia ecological land classification system, we determined keys to assign and map locations of PNVs across the province. These information sources help determine appropriate interventions at the stand and landscape level for implementing an ecological forestry framework.

7. Conclusions

In this paper, we reviewed methods to apply natural disturbance regimes to derive forest management guidelines. Then we described a novel approach for ecological forestry developed for Nova Scotia in response to a recent independent review of forest practices in Nova Scotia (Lahey 2018) call for more ecological forestry. Because Nova Scotia has multiple overlapping major disturbance agents including fire, hurricanes, windstorm, and insect outbreaks, we developed ‘pooled multi-rotation models’ that account for the effects of multiple disturbances from different agents and with varying disturbance severity. We used the current ecological land classification system to determine and map PNV community types, quantified cumulative natural disturbance regimes for each PNV, and used the natural disturbance regime parameters to derive management guidelines for each PNV community.

Ecological forestry implementation and improvement has several key information needs: 1) characterizing the distribution (proportion of area) affected by each disturbance agent and severity level, by PNV; 2) determining parameters of disturbance severity (% of living biomass killed) by PNV and stand, site, and disturbance factors; 3) specifically for windstorm, higher temporal resolution of data than 5-year PSP remeasurements, which fail to differentiate between windstorm and annual tree

mortality rates; 4) in the Nova Scotia context, better understanding of gap creation and gap succession dynamics, given that Tolerant Hardwood, Tolerant Mixedwood, Tolerant Softwood and other hardwood PNVs have low disturbance rates; 5) determining the degree of overlap of individual natural disturbance agents (i.e., do fires or increased windthrow follow hurricanes or spruce budworm outbreaks?); and 6) companion research to assess biodiversity responses to forest conditions to inform changes to current approaches. In the current paper, we assumed that disturbances were probably independent and thus high severity instances could be summed, and although there is some evidence to the contrary, few data exist to determine the degree of overlap.

Ecological forestry requires natural disturbance emulation, which requires knowledge and application of natural disturbance regimes to guide forest management. This general approach of determining natural disturbance regimes, calculating return intervals and MADRs and corresponding rotation lengths or entry times for each PNV forest community appears to be feasible and applicable to any region with a strong ecological land classification system and multiple disturbance agents.

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Table 1. Key concepts used to characterize and apply natural disturbances to ecological forestry.

Concept	Definition
Ecological Forestry ¹	A management philosophy that emphasizes the creation and maintenance of natural ecological conditions, within which, the provision of goods and services to meet the needs and objectives of land owners and society is achieved.
Natural Disturbance ²	Any relatively discrete natural event that causes tree damage and mortality, which releases growing space and resources.
Disturbance Agent ²	A particular driver of natural disturbance (e.g., fire or wind).
Disturbance Regime ²	The average behavior of a disturbance agent over a defined time period, characterized by key disturbance variables, i.e., spatial extent, severity, and return interval.
Spatial Extent	Total landscape area affected by a single disturbance agent event (e.g., wide-scale >500ha, medium-scale 500-50ha, small-scale <50ha)
Severity ³	Total amount of living tree biomass killed per unit of forest area during a single disturbance agent event (e.g., high >60%, moderate 60-30%, low <30%)
Return Interval ⁴	Average time elapsed between successive disturbance agent events, of a particular severity level, at the same place on the landscape (e.g., long-term >150 years, medium-term 50-150 years, short-term <50 years). It also represents the time required to disturb an area equivalent in size to the landscape.
Mean Annual Disturbance Rate ⁵	Amount of eligible forest area disturbed per year by a specific disturbance agent and severity level. It is the inverse of the return interval.
Rotation Length ⁶	The interval of time between regeneration and harvesting the full, mature stand. Usually associated with high-intensity, stand-replacing cutting activities (e.g., clearcutting) that lead to the creation of single- and multi-aged stand structures.
Entry Time ⁶	The interval of time between episodes of partial cutting. Usually associated with low- to moderate-intensity cutting activities (e.g., shelterwood or selection harvest silviculture methods) that lead to the creation of multi- and all-aged stand structures.

¹ Christensen et al. (1996); Seymour and Hunter (1999); Davis et al. (2001)

² White and Pickett (1985); Smith and Smith (2015)

³ Severity levels were designed to coincide with definitions of clear-cut and partial-cut harvesting intensities used by the Nova Scotia DLF (<https://novascotia.ca/natr/strategy/clear-cut-definition.asp>).

⁴ Return interval may also be interpreted as the time it would take for a disturbance agent to disturb an area equivalent in size to the landscape under consideration at a particular severity level.

⁵ 'amount' of area is usually expressed as a percentage. 'eligible' signifies that not all forest areas on a landscape are vulnerable to each disturbance, as some disturbance agents are tree species-specific (e.g., spruce budworm).

⁶ Ashton and Kelty (2018)

Table 2. Classes of soil drainage, soil texture, and topographic pattern and landform that are used to define ecosections in the Nova Scotia ecological land classification system. Ecosection names are depicted using a four letter code: 1st letter soil drainage, 2nd letter soil texture, 3rd and 4th letters topographic pattern and landform (modified from Neily et al. 2017).

Code	Description	Definition
Soil Drainage		
W	Well drained	Soils > 60% well drained
P	Poorly drained	Soils > 60% poorly drained
I	Imperfectly drained	Soils neither well or poorly drained
Soil Texture		
C	Coarse textured soils	Gravel, coarse sand, sand, loamy sand, coarse sandy loam
M	Medium textured soils	Sandy loam, fine sandy loam, very fine sandy loam, loam
F	Fine textured soils	Silt, sandy clay loam, clay loam, sandy clay, silty clay, clay
O	Organic	Decomposing plant material
Topographic Pattern and Landform		
DM	Drumlinoid	A pattern of elongated landforms caused by glacial ice movement (drumlins and flutes) often occurring in clusters
DS	Canyons and steep slopes	Sharply sloped terrain along rivers/streams or associated with hilly topography. Slopes usually 20-80%
FP	Floodplains, intervals, deltas	Areas adjacent to rivers and streams that are annually or periodically flooded and enriched by sediment
HO	Hummocky	A series of small rounded hills with a gentle slope usually 15% or less
KK	Hills	A series of knobs and knolls with moderate to steep slopes between 5-30%. Relief amplitude ranges from 15-60m.
RD	Ridges	A pattern of linear or curvilinear ridges of bedrock or glacial till origin
SM	Smooth or flat (level)	Land with no particular pattern, flat or very gently sloping. Slope generally < 1% (e.g., lake plain, open bogs, wetlands)

Table 3. Definition and overall area of each potential natural vegetation (PNV) forest community of Nova Scotia. Acadian and Maritime Boreal Zonal forest communities reflect regional climate norms and are not unduly affected by local extremes in site conditions (soil moisture and nutrients). Azonal forests result when a forest community cannot progress to the zonal climax due to local extremes in site conditions (wet or dry and (or) nutrient poor).

PNV forest community ¹	Typical species composition	Area	
		Ha	%
Acadian Zonal Forests (Ecoregions 300, 400, 500, 600, 700, 900, and Ecodistrict 220)			
Tolerant Hardwood	Sugar maple, beech, yellow birch. White ash ² and ironwood ² are common on richer sites. Red maple in the east and red oak in western NS may be included	1,257,700	22.8
Tolerant Mixedwood	Contains sugar maple, beech, yellow birch, red spruce, hemlock, or white pine. White spruce may be a component. Occasional species include red oak, white ash and ironwood. Pockets of hardwood or softwood forests may occur depending on slope position	407,124	7.4
Tolerant Softwood	Red spruce and hemlock with lesser amounts of white pine. Balsam fir usually present at some stage	1,134,071	20.5
Maritime Boreal Zonal Forests (Ecoregions 100, 800, and Ecodistrict 210)			
Coastal Spruce-fir	White spruce, black spruce, balsam fir forests occurring on well to imperfectly drained soils	304,375	5.5
Coastal Hardwood	Red maple & white birch with occasional yellow birch on well drained soils, inland from direct coastal exposure	22,787	0.4
Highland Fir	Balsam fir with lesser amounts of white spruce and white birch. Yellow birch & balsam fir form mixedwoods where Tolerant Hardwood slopes blend into Highland Fir	161,667	2.9
Azonal Forests (All ecoregions)			
Spruce-Pine	Black spruce often with a white pine canopy. White, jack and red pine often with some black spruce	1,485,718	26.9
Acadian Wet Coniferous	Black spruce, larch, and balsam fir on poorly drained soils. Red maple is a common associate	169,561	3.1
Maritime Boreal Wet Coniferous	Black spruce, white spruce, larch, and balsam fir on poorly drained soils	57,853	1.0
Floodplain	Late successional forests would have sugar maple with American elm ² and white ash ²	32,626	0.6
Non-forest			
Water	All freshwater	250,416	4.5
Other	Includes barrens, open wetlands, salt marshes, coastal beaches, dunes, urban areas	236,779	4.3
Grand Total		5,520,676	100.0

¹ PNV is closely synonymous with Forest Group (Forest Ecosystem Classification, Neily et al. 2013).

² American elm (*Ulmus americana* Augustine), ironwood (*Ostrya virginiana* (Mill.) K. Koch), white ash (*Fraxinus americana* L.)

Table 4. Frequency, mean, median, and maximum simulated fire size (ha) summarized by Potential Natural Vegetation classes. Simulations were based on lightning fire starts, with 9000 iterations using the BURN-P3 model (Parisien et al. 2005). See Figure A2 and Table S2 for more information.

PNV forest community	Frequency	Fire size (ha)		
		Mean	Median	Maximum
Acadian Zonal Forests				
Tolerant Hardwood	1,736	1,494	1,194	10,966
Tolerant Mixedwood	560	1,488	1,254	7,482
Tolerant Softwood	2,321	1,860	1,542	15,360
Maritime Boreal Zonal Forests				
Coastal Spruce-Fir	304	1,664	1,287	7,411
Coastal Hardwood	24	1,622	1,277	5,218
Highland Fir	311	2,240	1,988	8,058
Azonal Forests				
Spruce-Pine	3,194	2,248	1,862	14,568
Acadian Wet Coniferous	317	2,658	2,227	11,912
Floodplain	74	1,418	1,098	4,429
Maritime Boreal Wet Coniferous	123	2,891	2,617	9,440

Table 5. Percentage area of each PNV forest community by Ecoregion, along with total area per Ecoregion (ha). Names of the nine ecoregions in Nova Scotia (Neily et al. 2017) associated with numbers 100-900 are defined in Fig. 3.

PNV forest community	Area of PNV forest community by Ecoregion (%)								
	100	200	300	400	500	600	700	800	900
Acadian Zonal Forests									
Tolerant Hardwood		1.17	59.13	15.81	26.55	2.04	11.74		55.42
Tolerant Mixedwood		4.98	11.38	15.70	6.18	19.04	0.36		25.56
Tolerant Softwood			10.36	23.33	11.00	27.64	38.47		12.40
Maritime Boreal Zonal Forests									
Coastal Spruce-fir								65.45	
Coastal Hardwood								4.90	
Highland Fir	29.32	73.07							
Azonal Forests									
Spruce-Pine		3.41	15.78	32.62	47.88	34.88	32.48		4.59
Acadian Wet Coniferous		0.14	1.08	2.04	2.44	5.79	5.89		0.70
Maritime Boreal Wet Coniferous	40.23	13.56						2.66	
Floodplain		0.09	0.59		0.81	4.73			
Non-forest									
Water	2.79	1.70	1.58	6.74	2.16	1.48	8.10	5.11	0.41
Other	27.66	1.88	0.09	3.76	2.98	4.40	2.95	21.87	0.92
Area per Ecoregion (ha)	44,430	203,418	1,092,988	642,182	836,601	406,501	1,686,528	465,046	142,943

Table 6. The current percentage area of tree species cover of the top 12 species (95% of species cover provincially) for each PNV forest community as estimated by Nova Scotia's photo-interpreted forest inventory. The current percentage area values shown in bold font indicate species that are generally considered late successional and characteristic of that PNV forest community.

PNV Forest Community	Area of current tree species cover by PNV Community (%) ¹													
	SM	YB	RM	WB	TA	RS	EH	WS	BS	BF	WP	TL	OT ²	UC ³
Acadian Zonal Forests														
Tolerant Hardwood	12.73	11.04	16.36	8.43	2.79	7.41	1.57	10.62	5.95	14.91	1.62	1.88	4.69	10.19
Tolerant Softwood	4.09	2.92	19.56	5.32	4.43	17.78	1.88	4.54	10.75	11.88	7.33	2.51	7.01	11.52
Tolerant Mixedwood	7.62	6.88	18.33	6.65	6.05	13.19	1.87	8.52	5.53	14.8	1.04	2.48	7.04	15.03
Maritime Boreal Zonal Forests														
Coastal Spruce-Fir	0.29	1.03	16.58	3.97	0.96	4.23	0.08	11.46	28.99	20.46	1.11	6.62	4.22	10.23
Coastal Hardwood	0.49	4.28	9.05	3.74	0.04	1.07	0.00	12.25	24.11	33.87	0.06	7.11	3.93	14.39
Highland Fir	2.58	7.40	5.67	9.60	0.04	0.00	0.06	15.55	16.12	41.41	0.21	0.96	9.92	4.72
Azonal Forests														
Spruce-Pine	1.10	1.79	17.66	4.05	4.22	10.91	1.04	3.83	23.8	12.67	7.94	6.07	4.92	9.92
Acadian Wet Coniferous	0.88	1.12	16.06	2.45	2.92	8.70	0.66	3.63	31.04	9.77	7.88	9.73	24.69	5.80
Floodplain	2.84	1.79	17.39	4.17	8.60	6.61	1.04	19.73	9.86	12.15	1.11	6.90	7.81	15.26
Maritime Boreal Wet Coniferous	0.26	1.51	6.29	3.72	0.38	1.75	0.03	11.60	31.42	37.15	0.86	4.59	0.44	3.55
Total Area of Cover (ha x 1000)	184.1	171.1	583.9	195.5	120.5	433.8	41.9	277.4	574.9	533.7	168.7	133.3	206.2	373.5

¹ SM: sugar maple; YB: yellow birch; RM: red maple; WB: white birch; TA: large-tooth or trembling aspen; RS: red spruce; EH: eastern hemlock; WS: white spruce; BS: black spruce; BF: balsam fir; WP: white pine; TL: tamarack/eastern larch; OT: all other classified species in climax community.

² Common species in the OT (other) category that comprise 1% or more of cover include red oak, other spruce (mixed red and black spruce stands), American beech, ash species (typically white and sometimes black ash), grey birch, and red pine.

³ These total areas of major tree species exclude recent clearcuts and regenerating forest, which are placed in other categories by the forest inventory.

Table 7. Mean annual disturbance rates (MADR) for Nova Scotia PNV forest communities in three disturbance severity classes (low <30% of living biomass killed, moderate 30-60%, and high >60%; Taylor et al. 2020). Italics font indicates the primary disturbance rate by a given disturbance agent (fire, windstorm, hurricane, or spruce budworm outbreak), in cases where disturbance rates vary with species composition or disturbance intensity. Bold font indicates the primary disturbance, or if there is none, the combined disturbance rate.

PNV forest community	Mean annual disturbance rate by PNV forest community (% yr ⁻¹)				
	Fire ¹	Windstorm ²	Hurricane ³	Spruce budworm ⁴	Total combined severe disturbances ⁵
Tolerant Hardwood	<i>0.20</i>	2.4 low, 0.35 mod., high <i>0.0</i>	29% 0.09, 46% 0.14, 25% <i>0.08</i>	Not applicable	0.20- 0.28
Tolerant Mixedwood	<i>0.20</i>	3.9 low, 0.49mod., high <i>0.0</i>	33% 0.09, 39% 0.14, 28% <i>0.08</i>	0.5 (1.0 for RS, prorated by half as MW)	0.25- 0.53
Tolerant Softwood	<i>0.33</i>	2.4 low, 0.31mod., high <i>0.0</i>	33% 0.09, 31% 0.14, 36% <i>0.08</i>	0.4 for RS	0.3- 0.61
Floodplain	<i>0.20</i>	0.0 low, 0 mod., high <i>0.0</i>	29% 0.09, 46% 0.14, 25% <i>0.08</i>	Not applicable	0.2- 0.28
Highland Fir	<i>0.33</i>	1.1 low, 0.22mod., high <i>0.0¹</i>	34% 0.09, 31% 0.14, 35% <i>0.08</i>	2.1 for BF	2.1 -2.51
Coastal Hardwood	<i>0.20</i>	7.7 low, 1.54mod., high <i>0.0</i>	29% 0.09, 46% 0.14, 25% <i>0.08</i>	Not applicable	0.28
Coastal Spruce-Fir	<i>0.33</i>	7.1 low, 1.28 mod., high <i>0.0</i>	34% 0.09, 31% 0.14, 35% <i>0.08</i>	1.5 for SPBF	1.16 -1.91
Spruce-Pine	BS-PI 0.5¹	3.6 low, 0.47 mod., high <i>0.0</i>	34% 0.09, 31% 0.14, 35% <i>0.08</i>	0.5 for BS	0.25- 0.75
Acadian Wet Coniferous	lowland BS 0.17	2.9 low, 0.29 mod., high <i>0.0</i>	34% 0.09, 31% 0.14, 35% <i>0.08</i>	0.5 for BS	0.25- 0.75
Maritime Boreal Wet Coniferous	lowland BS 0.17	0.0 low, 0 mod., high <i>0.0</i>	34% 0.09, 31% 0.14, 35% <i>0.08</i>	0.5 for BS	0.25- 0.75

¹ Fire disturbance rates were calculated based on return intervals of 500 yrs for Tolerant Hardwood, 300 yrs for Tolerant Softwood, and 200 yrs for Spruce-pine (Ponomarenko 2018; see data in Table S2). We assumed that Tolerant Mixedwood, Costal Hardwood, and Floodplain were the same 500 years as Tolerant Hardwood; and Highland Fir and Spruce-fir were the same as Tolerant Softwood (300 years), and lowland black spruce (BS) 600yrs (Ponomarenko 2018; Taylor et al. 2020).

² Windstorm MADR from Taylor et al. (2020) was 0.02% yr⁻¹ for high and moderate and 1.4% yr⁻¹ for low severity classes, resulting in return intervals of 5000 yrs and severity 71 yrs, respectively. However, based on a follow-up analysis of MADRs for this paper, using 2800 PSPs (see Table S2), MADRs for windstorm ranged from 0.00-7.69% yr⁻¹ among PNVs for low severity and 0.00% for both moderate and high severity classes. Assuming that some 5-year windthrow occurred from storm events (Table S2), the above moderate values of 0.0-1.54% yr⁻¹ resulted. In this plot analysis, low windstorm was assigned as 5-30% windthrow, to eliminate the many instances of <5% windthrow.

³ Hurricane return interval varied by severity (% of stand killed) classes: low 1111 years (0.09% yr⁻¹), moderate 714 years (0.14% yr⁻¹), and high 1250 years (0.08% yr⁻¹), for all of Nova Scotia. The first % number presented is the proportion of the PNV area with that level of disturbance (e.g., for Tolerant Hardwood, 29% of the area had low (0.09% yr⁻¹), 46% had moderate (0.14% yr⁻¹), and 25% had severe (0.09% yr⁻¹)). Data from surveys conducted following Hurricane Juan indicated a higher proportion of high severity windthrow area for Softwood and Spruce-balsam fir (35-36%) stand types than for Hardwood, Mixedwood, or Pine stand types (25%, 27%, and 29%, respectively) (Taylor et al. 2020).

⁴ Spruce budworm outbreak severity (% tree mortality) varies with host species: balsam fir (BF) >60%; white spruce (WS) and red spruce (RS) 30-60%; and black spruce (BS) <30%. Assuming a 40-year return interval and prorating area disturbed by host mortality rate (BF 85%, WS 60%, RS 40%, and BS 20%), MADRs were: BF 2.1% yr⁻¹; WS 1.5% yr⁻¹; RS 1.0% yr⁻¹; and BS 0.5% yr⁻¹. However, on mainland Nova Scotia, where RS mainly occurs, spruce budworm outbreaks severe enough to cause mortality mainly occur in the northern half of the province, so we have reduced the RS mortality rate from 1.0% to 0.4%. We assumed that spruce mortality was one-half moderate severity and one-half high severity.

⁵ The range of values for total combined disturbances reflects uncertainty as to whether the spatial extent of areas disturbed are exclusive to a given area or cumulative in the same area, such that the final % could never be more than the sum or less than the highest % from a given agent. The range therefore shows the maximum of a given agent on the low end (i.e., all disturbances happen in the same spatial extent) and the sum of all the %s on the high end (no disturbance happens in the same spatial extent of another).

Table 8. Summary of disturbance rates and return intervals for high, moderate, and low severity disturbances for each PNV forest communities. PNVs were ordered by cumulative high severity disturbance rate. See Table 7 for the source of specific values.

PNV forest community	High severity disturbances ¹		Moderate severity disturbances		Low severity disturbances ²	
	Disturbance rate (% yr ⁻¹)	Return interval (yrs)	Disturbance rate (% yr ⁻¹)	Return interval (yrs)	Disturbance rate (% yr ⁻¹)	Return interval (yrs)
Tolerant Hardwood			0.49	204	2.49	40
Floodplain	0.28	357	0.14	714	0.09 ³	1111 ³
Coastal Hardwood			1.68	60	7.79	13
Tolerant Mixedwood	0.53	189	0.88	114	3.99	25
Tolerant Softwood	0.61	164	0.34	294	2.49	40
Spruce-Pine			0.86	116	3.69	27
Acadian Wet Coniferous	0.75	133	0.68	147	2.99	33
Maritime Boreal Wet Coniferous			0.39	256	0.09 ³	1111 ³
Coastal Spruce-Fir	1.16	86	2.17	46	7.19	14
Highland Fir	2.1	48	0.36	278	1.19	84

¹ High severity disturbances (>60% of living biomass killed; Taylor et al. 2020) included fire, hurricane, and spruce budworm outbreaks. We assumed that fire resulted in all high severity disturbances, but that spruce budworm outbreaks in spruce species were one-half high severity and one-half moderate severity disturbances.

² Low severity disturbances (<30% of living biomass killed) consisted of windstorms (rate of occurrence 0.0-7.7% yr⁻¹, depending upon PNV – see Table 67 and Hurricanes (29-34% of the area, depending upon PNV, had a low severity response to Hurricane Juan; Table 7) with a disturbance rate of 0.09% yr⁻¹ (Taylor et al. 2020).

³ The very low disturbance rates and high return intervals for Floodplain and Maritime Boreal Wet Coniferous PNVs low severity disturbances are likely under estimated (due to low plot samples, n=13 and 39, respectively, for windstorm damage; Table S2), but this is the best we have based on current data.

Table 9. Summary of PNV communities grouped by overall total disturbance severity (% of area killed, in classes of low <30%, moderate 31-60%, high >60%) and resulting stand-level age class distribution.

PNV forest community	Primary high severity disturbance agents	% of area killed in 3 mortality classes from all disturbances			Stand-level age-class distribution
		Low (<30%)	Moderate (30-60%)	High (>60%)	
Tolerant Hardwood, Floodplain, Coastal Hardwood	None ¹	100 ¹	0	0	All-aged
Tolerant Mixedwood	None ¹	100 ¹	0	0	All-aged
Tolerant Softwood	Wind, fire, spruce budworm	50 ²	50 ²	0	All-aged
Spruce-Pine, Acadian and Maritime Boreal Wet Coniferous	Fire, spruce budworm	0	60 ³	40 ³	Multi-aged
Coastal Spruce-Fir	Wind, spruce budworm	0	40 ³	60 ³	Multi-aged
Highland Fir	Spruce budworm	0	20 ⁴	80 ⁴	Single-aged

¹ No disturbance predominates in the Hardwood and Mixedwood PNVs, but there are infrequent fires and hurricanes (disturbance rates 0.20% and 0.08% yr⁻¹, respectively) and spruce budworm partial mortality in the spruce-fir component of the Mixedwood PNV. As a result, the overall PNV had all or most area with low (<30%) mortality from severe disturbances.

² Tolerant Softwood has a mix of low and moderate severity disturbances, with partial mortality resulting from spruce budworm outbreaks plus infrequent fire and hurricanes.

³ Spruce-Pine, Acadian and Maritime Boreal Wet Coniferous, and Coastal Spruce-Fir PNVs have moderate disturbance levels from spruce budworm outbreaks and fire.

⁴ Highland Fir is dominated by moderate and high severity disturbances from spruce budworm outbreaks, with mortality level dependent upon host species (balsam fir > white spruce > red spruce > black spruce), and infrequent fires and hurricanes.

Table 10. Pooled multi-rotation model parameters for each PNV for moderate and low severity disturbances. Although Fig. 10 graphed the multi-models for high severity disturbances for each PNV (primarily for illustrative purposes), here only the model parameters are provided for each severity level and PNV. These include the target mean annual disturbance rates (MADR) and return intervals (RI) for each PNV (from Table 8), along with the pooled multi-model parameters for each PNV, including the approximate percent land area allocations, MADR and entry time (ET) solutions. See section 2.3.2 and Fig. 2c for further explanation on how parameters are used to model PNV disturbance rates.

PNV forest community	Moderate Severity Disturbance (30-60% mortality)					Low Severity Disturbance (<30% mortality)				
	Target rates		Proposed area-weighted rates ¹			Target rates		Proposed area-weighted rates ¹		
	MADR (% yr ⁻¹)	RI (yrs)	Approx. area (%)	MADR (% yr ⁻¹)	ET (yrs)	MADR (% yr ⁻¹)	RI (yrs)	Approx. area (%)	MADR (% yr ⁻¹)	ET (yrs)
Tolerant Hardwood	0.49	204	55	0.67	150	2.49	40	40	4.00	25
			25	0.33	300			35	2.00	50
			20	0.17	600			25	0.80	125
Floodplain	0.14	714	50	0.20	500	0.09 ²	1111	25	0.20	500
			30	0.10	1000			45	0.07	1500
			20	0.05	2000			30	0.03	3000
Coastal Hardwood	1.68	60	50	2.50	40	7.79	13	60	10.0	10
			30	1.11	90			30	5.00	20
			20	0.50	200			10	3.33	30
Tolerant Mixedwood	0.88	114	55	1.25	80	3.99	25	65	5.00	20
			30	0.50	200			25	2.50	40
			15	0.25	400			10	1.25	80
Tolerant Softwood	0.34	294	45	0.56	180	2.49	40	55	3.33	30
			30	0.22	450			30	1.67	60
			25	0.11	900			15	0.83	120
Spruce-Pine	0.86	116	55	1.25	80	3.69	27	55	5.00	20
			30	0.44	225			30	2.50	40
			15	0.25	400			15	1.25	80
Acadian Wet Coniferous	0.68	147	45	1.11	90	2.99	33	55	4.00	25
			35	0.40	250			30	2.00	50
			20	0.20	500			15	1.11	90
Maritime Boreal Wet Coniferous	0.39	256	45	0.63	160	0.09 ²	1111	25	0.20	500
			30	0.27	375			45	0.07	1500
			25	0.13	800			30	0.03	3000
Coastal Spruce-Fir	2.17	46	55	2.86	35	7.19	14	50	10.0	10
			35	1.54	65			35	5.00	20
			10	0.71	140			15	2.50	40
Highland Fir	0.36	278	45	0.57	175	1.19	84	50	1.67	60
			30	0.25	400			35	0.83	120
			25	0.11	900			15	0.42	240

¹ Proposed area allocations and return intervals are rounded-up to nearest 5th percent and year, respectively, for practical purposes and are meant to represent approximate areas to be allocated under different MADR regimes.

² These values are likely underestimated and represent the minimum expected disturbance rate based on limited data availability.

Fig. 1. Flow chart of the key steps in defining and mapping potential natural vegetation (PNV) across the province of Nova Scotia, defining natural disturbance regimes for each PNV, and using pooled multi-rotation models to determine ecological forestry targets.

Fig. 2. Hypothetical stand age class distribution on a managed landscape resulting from a) 100-year harvest rotation length, versus b) 100-year natural disturbance return interval, which considers the quasi-random occurrence of natural disturbance, after Van Wagner (1978) and Seymour and Hunter (1999). Part c) illustrates how the negative exponential stand age distribution produced by nature may be approximated through forest management by partitioning the landscape into areas (grey rectangles) managed under different harvest rotation lengths. Part c) shows an example of landscape-level age class distribution targets, with proportions of landscape and rotation length represented by three classes (grey rectangles).

Fig. 3. Location of the study area and ecoregions of Nova Scotia (Neily et al. 2017).

Fig. 4. Edatopic grid of PNV forest community ecosites for A. Acadian and B. Maritime Boreal Forests.

a) Ecoregion 300 – Nova Scotia Uplands

Fig. 6. Lightning and lightning fire occurrence in Nova Scotia. A. Lightning flash density per year (flashes $\text{km}^{-2} \text{yr}^{-1}$) analyzed in 10 km cells, for January-December 1999-2018 (provided by L. Mainwaring and W. Burrows, Canadian Lightning Detection Network, Environment and Climate Change Canada, Oct. 5, 2020); and B. lightning fires in Nova Scotia from 1988-2019, depicted with a default kernel density overlay to help visualize.

Fig. 7. Map of PNV forest communities in Nova Scotia, assigned to ecosections

Fig. 8. Locations and relative amount of individual PNV forest communities in Nova Scotia. Areas and % area of each community are summarized in Table 3.

Fig. 9. Locations of common tree species, in 10% cover classes, as estimated from Nova Scotia's photo-interpreted forest inventory.

Fig. 10. Pooled multi-rotation models for each PNV for high severity disturbances. Models follow the same hypothetical framework described in Section 2.3.2 and Fig. 2c, where the solid black lines illustrate the negative exponential time since disturbance (TSD) distributions for each PNV, based on the high severity mean annual disturbance rates (MADR) shown in Table 6. The grey rectangles and corresponding 'proposed area-weighted rates' for each PNV suggest how forest management could partition the PNV landscape into land areas managed under three different harvest rotation lengths (RL). For each PNV, the sum of the percent land area allocations multiplied by the MADR for each allocation (i.e., the area-weighted rates) equals the overall target MADR for that PNV.

Appendix

Table A1. The Nova Scotia Ecological Land Classification (Neily et al. 2017) has five levels, describing the variety of terrestrial ecosystems across the province at ecologically relevant scales. The broadest scale division is the ecozone, which is further subdivided into finer scaled ecoregions, ecodistricts, ecosections and ecosites. Each unit is distinguished by various factors including: climate, topography, landform, soils, vegetation, nutrient and moisture regimes, as well as site characteristics (aspect, steepness, and slope position). Finer levels of the classification provide additional detail about the ecosystem (modified from Neily et al. 2017).

Ecological Unit	Map Scale	# of Units	Criteria For Delineating Units	Mapped
Ecozone	1:1 000 000	1	Global or continental climate as reflected by vegetation	Yes
Ecoregion	1:500 000	9	Provincial climate as expressed through soils and vegetation	Yes
Ecodistrict	1:250 000	39	Subdivisions of ecoregions characterized by distinctive assemblages of relief, geology, landform, soils and vegetation	Yes
Ecosection	1:50 000	707 *	Enduring features of the ecodistrict such as soil drainage, topography, landform and soil texture. These usually arrange as repeating assemblages in the ecodistrict.	Yes
Ecosite	1:10 000	N.A.	A uniformity of parent material, soil moisture and nutrient regimes and vegetation as expressed by slope, slope position, aspect and exposure	No

* Ecosections and ecosites are the only two types of units that are not coded uniquely within higher order levels of the ELC. For example, WCHO (an ecosection unit) may be found in any ecodistrict or ecoregion. However, each occurrence of WCHO is more similar within a given ecodistrict than it is among different ecodistricts or ecoregion.

Figure A1. Decision keys of method of assignment of potential natural vegetation (PNV) forest community by ecosection, based on drainage class, landform/soils, and sometimes ecodistrict for four Acadian ecoregions: a) Ecoregion 400, b) 500, c) 600, and d) 900. Numbered superscripts on ecosection refer to specific ecosection interpretation notes by Ecoregion, listed in the supplementary material.

a) Ecoregion 400 - Eastern

b) Ecoregion 500+220 – Northumberland/Bras D’Or, Victoria Lowlands

Figure A1 continued

c) Ecoregion 600 – Valley & Central Lowlands **d) Ecoregion 900 – Fundy Shore**

Figure A2. Burn-P3 (Parisien et al. 2005) fire simulations: a) relative lightning ignition grid values; b) burn probability; and c) total area burned in 3,000 iterations of 3 lightning-caused fires per iteration (total 9,000 fires) in Nova Scotia.

Table A2. Windthrow mean annual disturbance rates (MADR) by PNV forest community and severity class, determined from 2800 PSPs measured from 2008-2017.

PNV forest community	No. plots	MADR (% yr ⁻¹) by severity class ^{1, 2}			Median windthrow by severity class (%)	
		<5%	5-30%	>30%	<5%	5-30%
Tolerant Hardwood	741	97.57	2.43	0.35	0.57	7.38
Tolerant Mixedwood	207	96.14	3.86	0.49	0.72	6.91
Tolerant Softwood	653	97.55	2.45	0.31	0.56	6.24
Floodplain	17	100.0	0.00	0.00	0.29	-
Highland Fir	93	98.92	1.08	0.22	0.42	6.84
Coastal Hardwood	13	92.31	7.69	1.54	0.34	13.04
Coastal Spruce-Fir	141	92.91	7.09	1.28	0.62	7.20
Spruce-Pine	779	96.41	3.59	0.47	0.67	6.37
Acadian Wet Coniferous	68	97.06	2.94	0.29	0.84	8.90
Maritime Boreal Wet Coniferous	39	100.0	0.00	0.00	0.57	-

¹ Based on annualized calculation of MADR (i.e., 5 year periodic values ÷ 5), no PNV forest communities had >30% windthrow disturbance rates. But if we assume that some 5-year windthrow values resulted from storm events, the above >30% column values result. We also divided the low <30% severity class into <5% and 5-30%, to better reflect the prevalence of very low (largely single tree) windthrow. Median windthrow values indicate that even within the <5% and 5-30% classes, most values are lower than the midpoint.

² Methods: To evaluate windthrow disturbance rates caused by windstorms (not hurricanes), we used Nova Scotia’s extensive forest PSP network, consisting of 3,250 circular plots (400 m²) randomly located across Nova Scotia forests. Plots are remeasured by NSDLF every 5 years, with some measurements extending back to the 1960s; however, detailed measurement of windthrow did not begin until after 1998. To remove windthrow caused by hurricanes, we only used measurements conducted after 2008 (which avoided windthrow from Hurricane Juan in 2003) and selected the most recent census for each plot. Only plots that contained at least 10 living trees (stems > 9.0 cm DBH) were included to avoid sampling very young, regenerating forest stands. This provided 5-year measurement histories of windthrow for 2,800 randomly distributed PSPs across the province, measured from 2008-2017. Windthrow estimates for each plot were obtained by tallying the number of downed trees (with an elevation angle <45°) and stem-broken trees since the last census and calculating the proportion of basal area impacted. This proportion was divided by the number of years since the last census to derive the mean annual windthrow disturbance rate for each plot. Plot estimates were averaged by PNV forest community