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Management of forest regeneration in boreal and temperate deer–forest systems: challenges, guidelines, and research gaps

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Abstract. Heavy browsing pressure from large ungulates is a multicontinent phenomenon that causes regeneration failure of many palatable tree species and induces important socioeconomic and ecological impacts in forest ecosystems. The development of forest management practices that address adequately this issue, however, remains scarce and challenging because (1) large herbivores are both a resource and a source of disturbance; (2) the management of forests and ungulate populations remains largely disconnected in practice; and (3) we still lack a good understanding of the role of critical factors, especially deer densities, vegetation attributes, and their interactions, on the magnitude of browsing damages on forest regeneration. We bring new insights into these challenging issues by critically reviewing the current methods used by managers and conservationists to mitigate deer impacts on forest regeneration, emphasizing the spatial scale at which these methods are undertaken. Specifically, we review management actions at multiple scales on both deer populations (e.g., hunting) and vegetation (e.g., silvicultural treatments) that are common to most deer–forest systems and, for that reason, deserve priority investigation. We identify strengths and limitations of current management actions and highlight the main research gaps. Based on this review, we propose a new integrated management scheme that explicitly addresses: (1) the integration and prioritization of management actions, (2) the development of adaptive management plans, and (3) the participation of stakeholders. Conflicting demands by different stakeholders have challenged the effectiveness of management strategies in deer–forest systems. To reverse this situation, we advocate for a shift of paradigm and the development of integrated strategies that (1) bridge the gap between management actions and the design of in situ experiments and (2) coordinate actions at multiple spatial scales on both deer populations and forests. We propose a new framework informed by key objectives and grounded in the adaptive management paradigm to support this transition, and suggest a research agenda for the next decade(s).

Key words: browsing; deer; deer hunting; deer management; deer overabundance; forest management; herbivory; large herbivores; saplings; seedlings; silviculture; tree regeneration; ungulates.

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Introduction

The current high abundance of large cervid species (i.e., including white-tailed deer *Odocoileus virginianus*, black-tailed and mule deer *Odocoileus hemionus*, red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, fallow deer *Dama dama*, sika deer *Cervus nippon,* and moose *Alces alces*), hereafter deer, is a multicontinent phenomenon that impacts the functioning of many natural and managed forest ecosystems (Fuller and Gill 2001, Ward 2005, Takatsuki 2009, Apollonio et al. 2010, Austrheim et al. 2011, Nugent et al. 2011, Chollet and Martin 2013, Nuttle et al. 2013). The main causes for abundant deer populations include a decrease in the abundance of natural predators and hunters, milder winters, an increase in young forests, the introduction of individuals outside their native range, and changes in deer management (e.g., harvest rates; Côté et al. 2004, Milner et al. 2006). Failure to regenerate palatable trees, shrubs, and ground layer plant species following heavy deer browsing is now a common pattern in many temperate and boreal forest ecosystems of North America (Rooney 2001), Europe (Speed et al. 2013, Schulze et al. 2014), Asia (Takatsuki 2009), and Oceania (Wardle et al. 2001). High herbivore densities may shift trajectories of forest succession (Hidding et al. 2013) and cause substantial losses to the forest economic sector (Ward et al. 2004). The severity of deer browsing on vegetation may also alter biogeochemical cycles (Persson et al. 2005) and plant–soil feedbacks (Kardol et al. 2014) and induce cascading effects on organisms that depend on the composition and structure of understory plant communities such as litter mesofauna (Wardle et al. 2001), macro-invertebrates (Brousseau et al. 2013), birds (McShea and Rappole 2000), and mammals (Côté 2005). Given the spatial extent and the strength of ecological and economic impacts caused by overabundant deer populations, the development of sound management techniques aiming at successfully establishing forest regeneration becomes increasingly important.

While our understanding of the magnitude and direction of impacts caused by deer on forest ecosystem dynamics has greatly improved in the last decade, much remains to be done for translating this knowledge into integrated forest management practices. Part of the challenge originates from the fact that large herbivores at high density are both a resource and a source of disturbance in forest ecosystems. Reducing herbivore populations to low density is not only technically difficult, but might also be unacceptable from a social and economic point of view in regions where hunting provides significant incomes (Wam and Hofstad 2007). On the other hand, overabundant populations prevent the establishment and height growth of palatable tree species, which may disrupt forest ecosystem dynamics and cause substantial economic losses for the forest industry. Along these two extremes, wildlife and forest resource managers face a common challenge of establishing trade-offs to balance social, economic, and ecological services of forest ecosystems.

Here, we critically review the current methods used to manage impacts caused by overabundant deer populations on forest regeneration of boreal and temperate forests. The objectives of this essay are threefold. First, we compare empirical results from contrasted geographical regions to identify which management actions on deer populations and forest vegetation, alone or in combination, appear promising (or not) to limit damages caused by deer on forest regeneration. Second, we identify gaps in knowledge regarding the efficiency of management practices, with a particular focus on the spatial scale at which management actions on deer and vegetation are undertaken (Fig. 1). We emphasize factors that are likely common in the majority of deer–forest systems and, for that reason, deserve priority investigation. Last, we discuss key challenges and further improvements in the management of forest ecosystems in the presence of overabundant deer populations.

Actions on Abundant Deer Populations

Managers and conservationists can act directly on the abundance and spatial distribution of herbivore populations to reduce their negative impacts on forest regeneration. Actions can be undertaken at a local scale to reduce immediate impacts on vegetation or at a regional scale to manage herbivores at the ecosystem level (Fig. 1; Côté et al. 2004). Local actions are generally related to stands with high socioeconomic or ecological values such as habitat of endangered

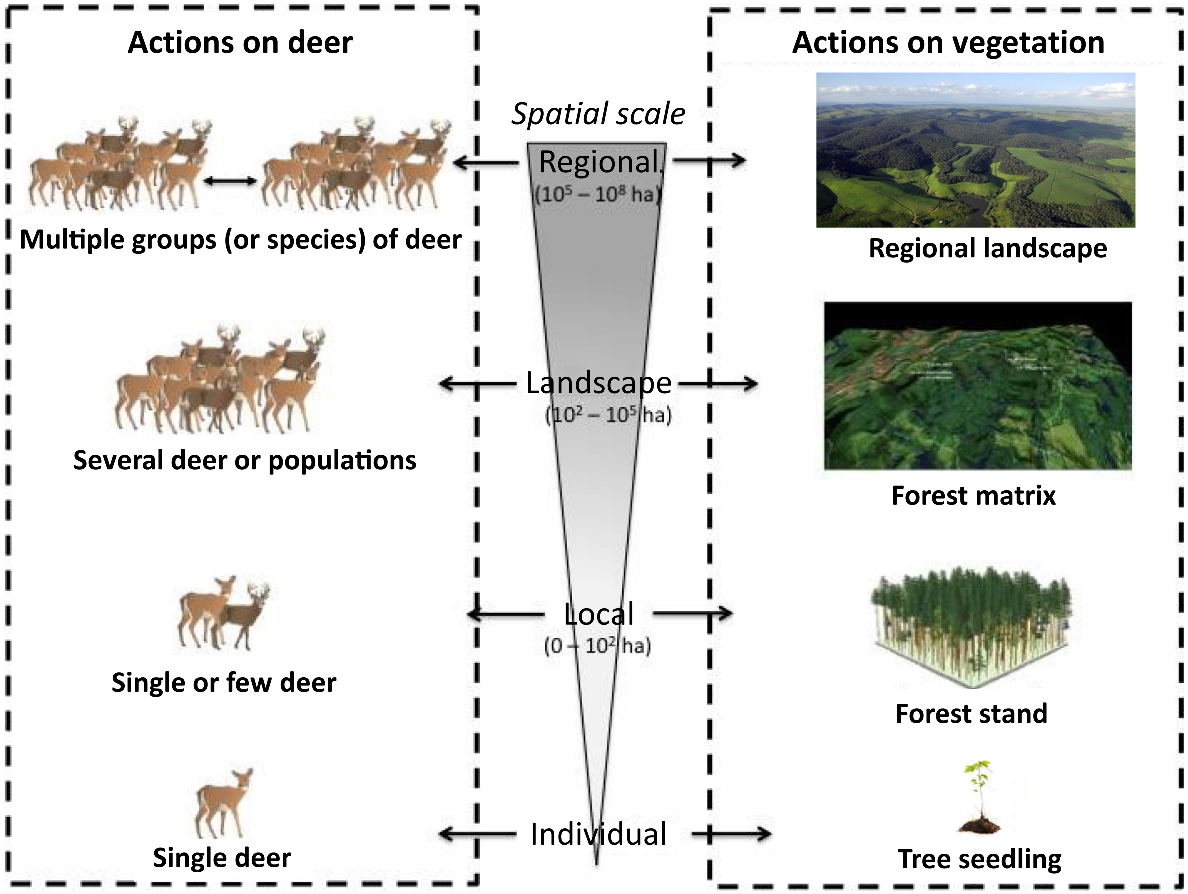

Fig. 1. Hierarchical structure of actions on deer populations and forest vegetation as a function of spatial scales (from individual to the regional level).

species, exceptional forest ecosystems, tree nurseries or noble tree plantations, or suburban forests. Sharpshooters have been successfully used in lethal control programs in suburban areas where sport hunting is limited due to legal constraints, safety, or public acceptance (Doerr et al. 2001). For the same reasons, alternative lethal controls such as poisoning are rarely used with cervids. Non-lethal methods include fertility control and relocation as well as chemical, physical (e.g., reflector and sound devices), or biological (e.g., dogs, hunting for fear) deterrents.

Fertility controls have been applied to wild cervids using chirurgical sterilization, subcutaneous hormonal implants, remote intramuscular injection of hormones or immunocontraceptive vaccines, and baiting with oral doses of synthetic steroids (Côté et al. 2004). Yet, these methods require invasive manipulation or repeated injections, limiting them to captive or small localized populations of free-ranging animals.

As with fertility control, relocation involves expensive and time-consuming capture sessions. Relocation also requires release sites capable of providing an alternative habitat for moved animals, but still the poor body condition of individuals in overabundant populations may lead to high postmanipulation mortality. Côté et al. (2004) summarized the factors limiting the effectiveness of chemical and physical deterrents (e.g., reflector and sound devices) in the context of overabundant populations of cervids: They may work at local spatial scale over the short term (i.e., days and weeks) but are generally not cost-effective in the medium to long term. Hazing with trained dogs has also been successfully used to influence space use by elk (Walter et al. 2010). Increasing disturbance in regenerating forests through more aggressive hunting practices (i.e., hunting for fear) involving more hunting on foot and with dogs, longer hunting seasons, and hunting of juveniles has also been proposed (Cromsigt et al. 2013) and has so far lead to some successes in improving plant regeneration over the short term (Le Saout et al. 2014). More field experiments are needed to assess the efficiency of hunting for fear to mitigate deer impacts on forest regeneration over the medium and long terms (e.g., 5–10 yr).

At the regional scale, managers can also act directly on large herbivores using different forms of hunting such as sport hunting, culling, and commercial harvesting. Sport hunting is often considered the most effective and socially acceptable tool to control populations over large areas (Stedman et al. 2004). It has been shown to reduce damage to forest ecosystems in many regions of the world (Hothorn and Müller 2010, Wright et al. 2012, Chollet et al. 2016). Despite recent decreases in the number of hunters in some areas, the number of individuals practicing this activity globally remains high (Brown et al. 2000). Hunters use a large proportion of the land, and while contributing to reduce the number of animals, they also have a positive impact on the economy (Conover 1997). Maintaining the interest of hunters may also interfere with management goals seeking a reduction in the population as hunter participation is correlated with population abundance (Fryxell et al. 2010). Regulations (e.g., bag limit, length of the season) can be readily changed and rapidly implemented to increase the impact of hunting on deer numbers. Selective harvesting can also be used to increase the efficiency of hunting as a management tool (Nugent et al. 2011). For instance, several agencies are now encouraging the harvest of females to reduce the productivity of populations as survival of adult females is a key parameter in the population dynamics of deer (Coulson et al. 2004). Moreover, the philopatric behavior of female deer has been hypothesized to increase the temporal window of opportunity for forest regeneration following intense localized harvesting (Porter et al. 1991). This hypothesis has been proposed for white-tailed deer (Sage et al. 2003) but has so far received limited support at high deer densities (Miller et al. 2010, Simard et al. 2013), likely because female dispersal rates increase with deer density (Lutz et al. 2015).

In most jurisdictions, hunting is limited to specific seasons. When sport hunting is not sufficient to reduce deer populations, certain agencies may use culling at a regional scale, most often using professional hunters (Kilpatrick et al. 1997). For example, this is a common strategy for red deer in Scotland and several species of introduced herbivores in New Zealand. Large quotas are attributed and culled quickly. Alternatively, commercial hunting may occur using a similar approach. A problem with commercial hunting is that the populations need to remain high to allow economic sustainability. It also facilitates poaching because poachers then have a market to sell meat. It thus requires an efficient tracing system for venison.

In any management scenario, however, a key point is that hunting must be sustained over long time periods to be effective because of compensatory reproduction occurring at low density (Gaillard et al. 2000). Certain deer species are very plastic and may respond quickly to reduced density and increase the proportion of twins produced while reducing age at primiparity (white-tailed deer: Simard et al. 2008, moose: Gingras et al. 2014). Introduced species and those in high-quality habitat may also be more productive and require more aggressive harvesting.

Alternatively, actions can also be taken on populations of predators to affect large herbivores. Several attempts have been made to control populations of predators such as wolf (*Canis lupus*) and bear (*Ursus* spp.) to favor the increase or the maintenance of high herbivore densities (Boertje et al. 2010). Much less work, however, has been conducted to favor the (re)introduction or increase in predators to reduce cervid abundance. The most common situation includes the introduction of a predator in areas where it has been extirpated. For instance, the reintroduction of wolves in Yellowstone had a positive impact on plant regeneration through a top-down control of wolves on elk (Ripple et al. 2001). Accordingly, there is growing interest to reintroduce wolves in Scotland as an attempt to control the expanding populations of red deer (Nilsen et al. 2007). The recolonization of wolves in several European countries could also become an ecological driver for controlling the abundance and spatial distribution of deer populations in the future.

In practice, management of abundant deer populations is often impeded by antagonistic objectives because managers need to simultaneously maintain high deer population densities for hunters and wildlife observers while ensuring forest regeneration. The overarching goal and challenge in deer–forest management thus appear to be to maintain the highest deer densities compatible with natural forest regeneration.

Actions on Forest Vegetation

Aside from direct actions on animals, resource managers can also act directly on the structure and composition of forest vegetation, from seedlings to landscape (Fig. 1).

At the seedling scale, managers have used a panel of physical, chemical, and biological techniques for mitigating the impacts of deer on tree regeneration, with variable levels of success and opportunity costs. The success of regeneration is defined here as the minimum seedling density of different height classes that is required to reach a new stand compatible with specified management objectives. Physical protection of tree seedlings with plastic tubes and wire fencing prevents deer browsing, but high costs limit their use to highly valuable tree species within local sites (Côté et al. 2004). The presence of coarse woody debris can limit browsing of plants growing within aggregates (de Chantal and Granström 2007) or in the presence of tall fallen logs (Relva et al. 2008). Inversely, dispersion of logging slashes over regenerating areas is inexpensive, but its effect against deer browsing lasts only until terminal shoots become accessible to deer (Bergquist and Örlander 1998, Casabon and Pothier 2007, Pellerin et al. 2010), which narrows its scope to the early stage of tree seedling establishment (ca. height <50 cm). The effect of topical application of chemical repellents (i.e., sulfur, selenium, bittering agents), when effective against deer browsing, is currently restricted to short periods of time (ca. days or months; see Kimball et al. 2009). Fertilization is another chemical method that can increase the height growth of seedlings and decrease the time span during which terminal shoots are available to deer browsing. Its effectiveness against deer browsing, however, is limited possibly because fertilization can also increase the nutritive status of seedlings and their palatability for large herbivores (Burney and Jacobs 2011).

Aside from physical and chemical methods, plant associations may influence the likelihood of detection and/or vulnerability of focal plants to herbivores (Barbosa et al. 2009). The manipulation of the associated vegetation (e.g., herbs, grasses, ferns) has therefore been proposed as a mitigation measure against browsing on tree seedlings. Milchunas and Noy-Meir (2002) have proposed that favoring associational avoidance, for example, through an increase in the abundance of neighbor plant species with physical (e.g., spines) or chemical (e.g., toxic components) defenses, might protect tree seedlings from deer. This prediction has been supported by several empirical studies over the short term (≤5 yr; Smit et al. 2007, Vandenberghe et al. 2008, Harmer et al. 2010, Smit and Ruifrok 2011, Jensen et al. 2012, Perea and Gil 2014). The study of Bee et al. (2009) with red deer in New Zealand suggests that associational avoidance can be promising for seedling establishment over the long term as well. Inversely, an increase in the abundance of palatable neighbor plants provides alternative sources of forage that may dilute browsing risk on seedlings through contrasted associational defense (Atsatt and O'Dowd 1976). Studies with roe deer have supported this prediction: Roe deer ignored less palatable seedlings in favor of neighbor energy-rich palatable plants (Ward et al. 2008). Further experiments are needed to assess the role of plant associations to mitigate impacts of deer on tree regeneration, especially over the entire phase of seedling growth until the sapling stage. Whether the results from Bee et al. (2009) are applicable to other deer–forest systems also remains an open question.

At the stand scale, silvicultural actions can influence forage resources (i.e., quality, quantity, and distribution) and environmental conditions for deer through their effects on stand cover, understory vegetation, tree regeneration, stand structure, and forest edge properties (Wagner et al. 2011). Changes in certain stand characteristics may influence tree species predisposition to browsing. For instance, the use of partial cuttings generally results in the establishment of numerous tree seedlings and this large amount of seedlings established under the canopy has been hypothesized to saturate the needs of deer and to allow a sufficient amount of palatable seedlings recruiting in height beyond deer reach (Reimoser and Gossow 1996). This hypothesis, however, has so far received limited support, especially under high deer density that hindered the potential positive effects of increased light levels on vegetation growth (Beguin et al. 2009, Nuttle et al. 2013). Although costly, fencing at the stand level is sometimes used to allow advanced tree regeneration to become established before overstory removal, or to protect forest plants following a timber harvest.

Artificial regeneration through planting is another regeneration method at the stand scale that often results in severe damage to crop seedlings (Fahey and Lorimer 2013) compared with natural regeneration (Gill 1992). Artificial regeneration, however, offers the opportunity to select less susceptible species in the regeneration strata (Moore et al. 1999). Taking into account that large herbivores are most likely to feed on plants that are easier to find (Miller et al. 2006), managers can thus select planting stock types that represent the best trade-off between competitive potential and browsing risk (Faure-Lacroix et al. 2013).

In young stands within which a large proportion of tree crowns can be reached by deer, precommercial thinning could temporarily reduce browse availability by removing smaller, suppressed trees, while increasing the abundance of herbaceous species, shrubs, and tree regeneration over the long term (Kramer et al. 2006). The outcome of precommercial thinning on browsing risk, however, can also depend on neighboring plant assemblages at multiple spatial scales (Herfindal et al. 2015).

The indirect effects of silvicultural treatments are less studied, but changes in canopy composition and age as well as vertical and horizontal structures can influence the level of damages to established regeneration. For instance, in northern regions where snow depth is high, the use of selective thinning that reduces conifer cover decreases stand attractiveness for deer (Dumont et al. 1998) because hardwoods are less efficient than conifer species in intercepting snow. Similarly, an increase in clear-cut size has the potential to spare browsing in the center of clearcuts because of the increased predation risk (Kay 1993), yet when deer predators are absent, large clearcuts are inefficient in this regard (Casabon and Pothier 2007).

Aside from silvicultural treatments, supplementary feeding is intended to maintain stable ungulate populations while reducing seedling damage in neighboring stands (Putman 1996). Its use and efficiency, however, remain controversial as artificially maintaining high deer populations can lead to severe tree crop damage over the long term (Milner et al. 2014). For example, 15–20 yr of supplemental winter feeding has resulted in increased browsing of the commercially valuable Norway spruce (*Picea abies*) by moose (van Beest et al. 2010). Although browsing impacts at a scale <1 km followed an exponential decrease with distance from feeding stations, it did not show such a relationship at the landscape scale (1–10 km; Mathisen et al. 2014), stressing the need for considering both the time frame and spatial scale when implementing diversionary feeding strategies.

The spatial arrangement of forest cover and foraging habitat patches in managed landscapes can influence browsing damages locally (Ericsson et al. 2001, Miller et al. 2009). For example, a well-dispersed increase in small clear-cut areas can dilute food availability over the landscape and decrease the overall damage to tree regeneration over the short term (Miller et al. 2009). Over a longer period, however, a well-dispersed increase in food availability would likely increase ungulate abundance, thus increasing browsing damage (Kramer et al. 2006, Crimmins et al. 2010).

Forest edges can induce behavioral responses by deer that, in turn, influence vegetation predisposition to browsing. Linear and abrupt forest edges, such as those found between intact forest stands and clearcuts or roadsides, favor browsing risk in adjacent areas (Kay 1993, Reimoser and Gossow 1996, Gerhardt et al. 2013). In theory, forest management that favors smooth transitions between stands and low edge density at the landscape level should reduce browsing risk (Reimoser et al. 2009). But, most studies that have looked at edge effects on browsing damages were observational and did not account for deer density (Moore et al. 1999).

Increases in road densities following forest management activities, and their corollary impacts on human activities such as tourism, road traffic, and hunting, may affect the abundance of deer and their impacts on forest (Forman and Alexander 1998, Gerhardt et al. 2013). For instance, improving accessibility and visibility near roads increase hunting success (Lebel et al.

2012) and can contribute to decrease browsing impacts nearby. On the other hand, human activities may lead to decreased foraging time. It is therefore possible that the distance from disturbance sources influences vegetation predisposition to damages by deer.

Overall, the outcomes of actions on vegetation contain much uncertainty especially at higher spatial scales because (1) the number of interacting processes influencing deer browsing increases with increasing spatial scales; (2) experimental designs are more difficult to establish in practice at landscape and regional scales; and (3) uncontrolled factors, such as the level of deer densities, can strongly modulate the overall effect of actions on vegetation on deer browsing and forest regeneration success.

Toward Integrated Management of Actions on Deer Populations and Forest Vegetation

Experiments that have manipulated deer densities found thresholds above which the regeneration success of palatable species does not occur (Horsley et al. 2003, Tremblay et al. 2007). The impacts of deer on forest regeneration offset the effects of natural disturbance regimes on the dynamics of forests (Nuttle et al. 2013, 2014). These evidences support that the outcome of management actions on vegetation depends, at least in part, on deer densities. At high densities, the sole manipulation of forage resources and forest cover through silvicultural treatments is unlikely to ensure the recruitment of palatable tree species (Beguin et al. 2009, Matonis et al. 2011, Nuttle et al. 2013). It thus seems that the effectiveness of actions on vegetation is only possible when deer densities range from low to intermediate. Although this hypothesis has profound implications for the management of temperate and boreal forests, few attempts have been made to test it empirically using, for instance, more than two levels of intermediate deer density. Testing this hypothesis requires to manipulate jointly deer densities and vegetation attributes under replicated conditions.

Despite the need for such manipulation, local foresters responsible for designing and implementing forest management plans often continue to seek solutions to promote forest regeneration through the use of management actions on vegetation, without considering deer effects at a strategic level. On the other hand, decision-makers for deer management, often composed of a board of commissioners or executive-level political appointees (with potential inputs from advisory boards; see Fig. 3), often manage deer populations to maintain high wildlife-related values. The lack of integration between these disciplines occurs at different levels (e.g., governmental agencies, universities, stakeholders) and often translates into actions in the field that are cost-ineffective or only palliative over the short term. The use of supplementary feeding to maintain high deer densities and the use of final cuts in mature stands containing no tree regeneration layer because of severe deer browsing are good examples of such a lack of integration. Given the scale and magnitude of current deer impacts on forest regeneration patterns, reversing the situation has become a necessity in some regions. Interestingly, local initiatives that integrate deer management and forest management are increasing in number in both Europe and North America and will provide crucial inputs for the development of integrated management plans. An important step forward will consist in making results from these initiatives available to the scientific community, for instance, through peer-reviewed publications.

In regions where deer overabundance occurs, we advocate for an adaptive management approach of forests and deer populations where forest and deer management practices inform each other. Our suggestion relies on three main challenges: (1) the adhesion and active participation of stakeholders to the adaptive management cycle; (2) the explicit integration and prioritization of actions on deer populations and vegetation; and (3) the development of adaptive management plans repeatedly updated with the acquisition of new data and results from primary researches.

Challenge 1: participation of stakeholders and social dimensions of deer–forest management

The sustainable management of deer–forest systems is unlikely to succeed without a clear recognition that a shared understanding of the management process and objectives is essential among stakeholders. Deer–forest systems are socioecological systems characterized by incomplete scientific knowledge, uncertainty, and multistakeholder networks. These characteristics impose bridging the gap between science and policy, allowing policymakers and stakeholders, including society, to develop consensus about the functioning of the system and the goals of management (Gunderson 2015). To help define such management goals, scientists must implement research projects to stimulate reflection of respondents and then define achievable targets to meet the needs of society. When experiments can be controlled at small spatial scales and evaluated over short periods of time (i.e., years rather than decades), such as in deer–forest systems, adaptive management is considered the best approach to deal with socioecological systems (Westgate et al. 2013). The adaptive management cycle provides a holistic framework composed of six interrelated steps (see Fig. 3) aiming to design experiments and monitoring programs along current management schemes to test alternative hypotheses and to reach consensus among stakeholders about the main drivers in the system. In the case of deer–forest systems, this approach can reconcile divergent understandings among stakeholders about the process(es) responsible for tree regeneration failure, for example, when some advocate for a prevalence of bottom-up (e.g., soil conditions, seed abundance) vs. top-down (deer density) controls (Kuijper et al. 2010). Following Germestani and Allen (2015), adaptive management "tests explicitly predictions against observations, and allowing for iterative recalibration of the management process at predetermined decision points as learning occurs." Surprisingly, while adaptive management has been used extensively in a wide range of natural resource management contexts (McFadden et al. 2011), very few examples have been published in deer–forest systems (but see Kaji et al. 2010).

Deer–forest systems notably vary across the globe in terms of productivity, deer management policies, socioecological contexts, and law enforcement. For example, sale of venison shot by recreational hunters is common in Europe while forbidden in North America. Wildlife ownership is linked to land ownership in Europe while wildlife is a public trust in North America. Public land areas also are proportionally higher in North America than in Europe. Stakeholders may also have very different perspectives in regions where the respective deer species is native vs. introduced. Such differences prevent the use of common guidelines and compel policy- and decision-makers to be flexible. While adaptive management might not be a panacea in all situations, we advocate that it is a promising approach to guide the management of most boreal and temperate deer–forest systems, irrespective of the variation and particularities associated with local socioecological contexts. To be successful, however, important obstacles must be identified and assessed early in the process, such as (1) the neglect of social drivers during the decision-making process and (2) institutional and governance resistance.

All relevant stakeholders must be actively involved, committed to the process and willing to develop a "shared rationality" for adaptive management to succeed (Fig. 3). This might require educational support or training sessions on ecosystem functioning and management to specific stakeholders, especially when there is a lack of appreciation or concern about habitat conditions (e.g., for certain hunters, see Diefenbach et al. 1997). Hunters often tend to favor high deer densities to increase hunting success and economic outcomes over the short term (but see Cooper et al. 2015). This practice, however, can only be sustainable if the natural regeneration dynamics of forests characterizing a region is maintained across time and space. In other words, optimization of harvest decision of timber and deer should be contingent upon maintaining the integrity of ecological and evolutionary processes (a "shared rationality"). This principle applies whenever deer are native or introduced. In regions where deer were introduced, however, alterations in the structure and composition of the vegetation can be stronger than in their native ranges because coevolution did not occur between native plant species and exotic deer species. Managing overabundant introduced deer populations can therefore require more proactive responses potentially leading to increased deer harvest rates. In all cases, trust among stakeholders is the basis for decision-making and because hunters, foresters, and conservationists share the common interest of maintaining forest regeneration for timber, deer forage, and biodiversity, transparency and power balance should be integral parts of the decision-making process. If trust is lacking because of conflicting values, power imbalances, and/or stakeholders pushing agendas, the whole adaptive management process is unlikely to succeed and more traditional mechanistic approaches based on technical ecological considerations should be considered. This might include, for instance, deer population control programs using highly regulated hunts in complement to recreational hunting.

Challenge 2: integration and prioritization of actions

In addition to the implication of stakeholders in the management process, the integration of actions on vegetation with actions on deer populations under the constraint of limited resources requires prioritizing management efforts. When deer populations are overabundant and prevent the height growth of tree regeneration in forest landscapes where visibility and accessibility to hunters are low, management actions should be planned at a strategic level to modify habitat characteristics in order to increase deer harvest (Lebel et al. 2012). It is also at a strategic level that trade-offs between habitat changes and other management objectives (e.g., biodiversity conservation) can be identified and managed. In regions where deer are overabundant and visibility and accessibility to hunters are moderate to high, management efforts should first concentrate on lowering deer density. In practice, this implies delaying regeneration efforts (e.g., plantation and regeneration cutting) until deer densities are effectively reduced or, at a minimum, to do both simultaneously. It also implies that financial and human investments must be allocated to monitor deer population(s) and forest habitat trends. The choice of monitoring methods will depend on available resources and needed statistical precision (e.g., hunting/harvest statistics, ground vs. aerial surveys) and will likely differ among management situations. Using indicator of ecological changes including deer population trend, body condition and impact of browsing on forest habitat should be implemented to support the adaptive management of deer–forest systems (Morellet et al. 2007).

To reduce deer densities when necessary, hunting appears to be the method that provides the best trade-off among efficiency, social acceptance, and economic returns. Different forms of hunting, including hunting for fear (Cromsigt et al. 2013), can be used depending on management objectives, which provide flexibility to decision-makers. To be efficient, however, the current state of knowledge suggests that hunting activities must match the temporal and spatial scales of actions on vegetation. When hunting is used as a tool to decrease the number of deer, a key point is that hunting pressure should remain high and sustained over multiple years because of the compensatory reproduction occurring in deer (Simard et al. 2008). Failure to fulfill this requirement greatly increases the risk of regeneration failures (Jenkins et al. 2014), as seedlings need several consecutive years of height growth to surpass browsing height. Furthermore, hunting efforts must be prioritized spatially (1) in areas where deer overabundance is documented and (2) close to regenerating areas where the susceptibility to browsing is high. For instance, regeneration of understory shade-tolerant tree species requires more sustained hunting efforts because the growth of tree seedlings may be slower under these conditions than for shade-intolerant regeneration in open areas. The bulk of our approach thus relies on a revision of current practices toward a systematic and synchronized planning of silvicultural treatments (e.g., regenerating practices) with hunting efforts at multiple spatial and temporal scales (Fig. 2). This approach is currently used at an operational scale in the boreal forest of Anticosti Island (Canada), where landscapes (~7–10 km^2; Fig. 1) comprising clearcuts and residual forests are fenced and submitted to intense sport hunting to reduce white-tailed deer density followed by planting when necessary (Côté et al. 2014). Whether this approach applies in highly fragmented landscapes with many landowners and stakeholders remains an area of research that needs further investigations.

Challenge 3: data acquisition to support adaptive management

A third challenge that needs to be addressed is the acquisition of relevant scientific data to inform the effectiveness of an adaptive management scheme. Up to now, most studies that have investigated deer impact on forest regeneration patterns used simulated browsing, non-experimental designs, or experimental designs composed of

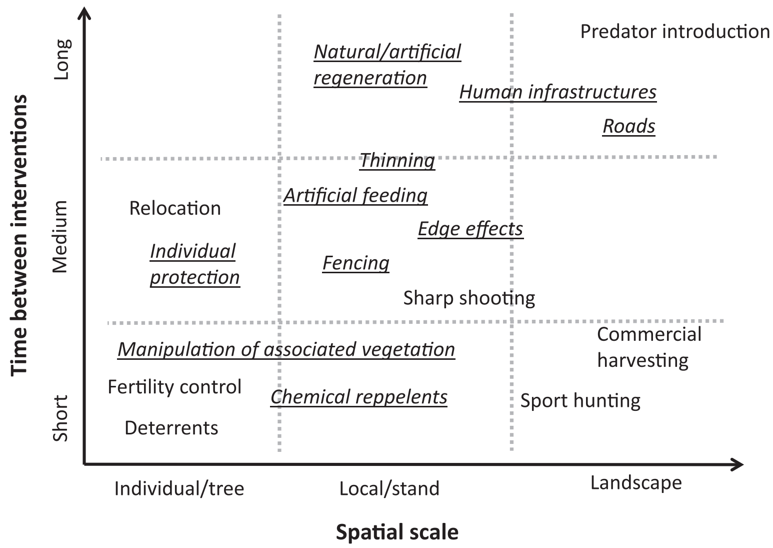

Fig. 2. Time between management interventions (italic and underscored type = actions on vegetation; other type = actions on deer) as a function of spatial scale in deer–forest systems.

replicated fenced and unfenced pairwise plots (Bergström and Edenius 2003, Côté et al. 2004). These studies need to be pursued as they bring valuable knowledge about the magnitude of deer impacts on forest regeneration and ecological communities. However, from a management perspective, the exclosure approach must be adapted to inform managers about the range of deer densities that is compatible with forest regeneration success over an assortment of ecological conditions and forest ecosystems (Hester et al. 2000, Bergström and Edenius 2003). Tackling this challenge in a rigorous manner requires the use of large-scale experiments that manipulate or control simultaneously for the interacting effects of various levels of deer density and vegetation attributes on forest regeneration success. At least two approaches can be used to meet these requirements: (1) the establishment of controlled deer densities factorial experiments (CDEs) and (2) the design of controlled experiments or sampling surveys integrated with the planning of management actions following adaptive management principles (Fig. 3). To our knowledge, the use of CDEs has been restrained so far to white-tailed deer in North America in the boreal (Anticosti Island, Canada: Tremblay et al. 2007) and northern hardwood (Pennsylvania, USA: Horsley et al. 2003) forests, whereas the design of experiments under adaptive management in deer–forest systems has been mostly published for sika deer in Japan (Kaji et al. 2010). It appears that very few adaptive management initiatives in deer–forest systems, if any, have considered hunting modalities associated with management actions as an experimental treatment in a priori planned experiments apart from the study conducted by Hothorn and Müller (2010) in Germany.

One key advantage of CDEs is to allow assessing the response of forest plants to known and controlled levels of deer density, removing the uncertainty associated with deer abundance estimators. CDEs, however, require high levels of financial and human investment (i.e., fencing, capture/relocation of animals, maintenance), which limits its use to small operational areas (e.g., <50 ha). On the other hand, the design of experiments under the adaptive management approach is more flexible and could be used by managers to create and maintain a gradient of deer densities through differential hunting pressure over a set of management units. Using such an approach, Hothorn and Müller (2010) showed that regions of Bavaria where the game management plans favored increased deer harvest had lower browsing damage than adjacent regions. Such flexible experiments might also be used to assess the potential of hunting for fear, which

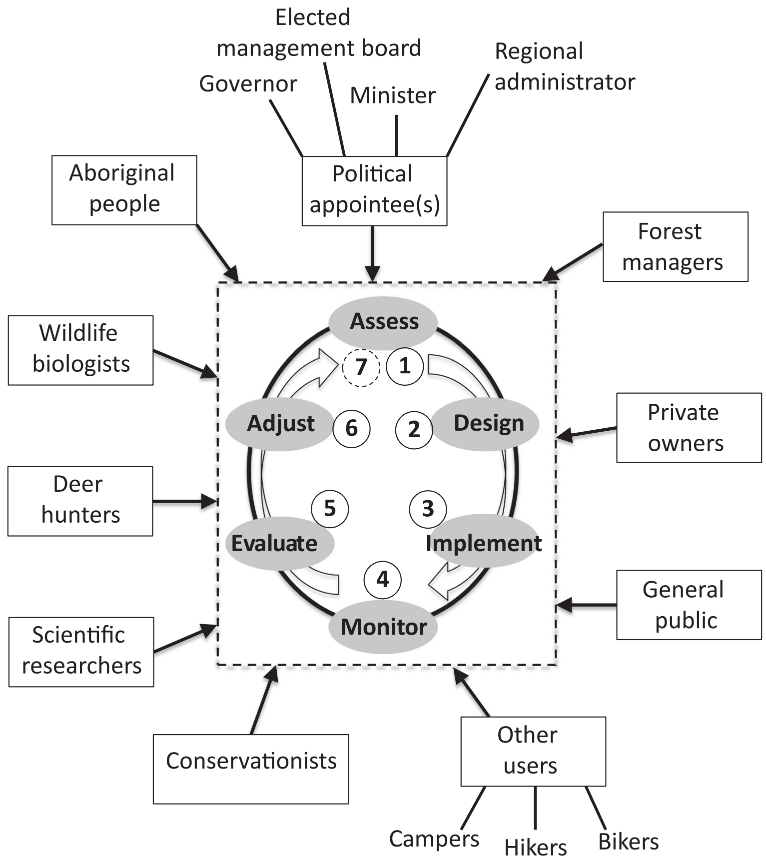

Fig. 3. The six phases cycle of adaptive management (from Gunderson 2015). The relevant stakeholders involved in the management of deer–forest systems in each phase of the cycle are represented. Political appointees are context dependent and can delegate their power to public servants. Definition of each phase (see table 10.1 in Murray et al. [2015] for more details): (1) *Assess:* Define the problem, build conceptual models, articulate hypotheses to be tested, explore alternative management actions, and identify/involve all relevant stakeholders; (2) *Design*: Design experimental treatments (with control and replications) to test alternative hypotheses, develop a monitoring plan, and secure multiyear budget; (3) *Implement*: Implement the design in the field and monitor the implementation; (4) *Monitor*: Implement the monitoring plan as designed; (5) *Evaluate*: Analyze the data, compare results with predictions/hypotheses, identify uncertainties and assumptions; (6) *Adjust*: Communicate results to stakeholders and decision-makers, document meaningful learning, and change actions or instruments based on what was learned. Restart a new loop in the cycle.

aims at inducing behavioral responses to deer (including their spatial distribution) to mitigate their impact on vegetation. If monitoring programs are designed at the same spatial scale than management actions, adaptive management has the potential to scale up valuable information on both deer and vegetation attributes at a scale relevant to resource managers (e.g., >1000 ha). The success of experiments in adaptive management, however, will likely depend on both the strengths of a well-designed quantitative monitoring program and the use of methods for estimating deer abundance and distribution, and for surveying vegetation that are standardized, accurate, and comparable among management units. Until now, CDEs have been used separately from adaptive management whereas they could often be complementary. For instance, in cases of adaptive management initiatives where hunters are reluctant to decrease deer densities below a given threshold, the use of partial CDEs that manipulate deer density but only at one level (e.g., low density) could be an alternative to the burden of full CDEs containing multiple levels of controlled deer densities. As suggested by Wisdom et al. (2006), adaptive management could also be used as a formal test for validating whether inferences gained from full CDEs apply to larger spatial scales.

Large-scale challenges require large-scale investigations and managers would greatly benefit from the establishment of a multicontinental network of CDEs and adaptive management initiatives encompassing a wide range of environmental conditions and deer species in temperate and boreal forests. Combining results from several CDEs and AM initiatives would bring new insights into the management efficiency of deer–forest systems where several deer species coexist. It would also allow testing whether the effectiveness of actions on vegetation at the stand and landscape levels is density dependent below certain thresholds of deer density, a fundamental question for managers that, as we outlined, remains unanswered.

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