Received: 23 May 2019 | Accepted: 3 February 2020
DOI: 10.1111/1365-2435.13544

REVIEW

Functional Ecology BRITISH ECOLOGICAL SOCIETY

Towards a framework for understanding the context dependence of impacts of non-native tree species

Sarah J. Sapsford[1] | Angela J. Brandt[2] | Kimberley T. Davis[3] | Guadalupe Peralta[1,4] | Ian A. Dickie[1] | Robert D. Gibson II[5] | Joanna L. Green[1] | Philip E. Hulme[5] | Martin A. Nuñez[6] | Kate H. Orwin[4] | Anibal Pauchard[7,8] | David A. Wardle[9] | Duane A. Peltzer[4]

[1]School of Biological Sciences, University of Canterbury, Christchurch, New Zealand; [2]Manaaki Whenua Landcare Research, Dunedin, New Zealand; [3]Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, MT, USA; [4]Manaaki Whenua Landcare Research, Lincoln, New Zealand; [5]Bio-Protection Research Centre, Lincoln University, Lincoln, New Zealand; [6]Grupo de Ecología de Invasiones, INIBIOMA, CONICET-Universidad Nacional del Comahue, Bariloche, Argentina; [7]Laboratorio de Invasiones Biológicas (LIB), Facultad de Ciencias Forestales, Universidad de Concepción, Concepción, Chile; [8]Institute of Ecology and Biodiversity (IEB), Santiago, Chile and [9]Asian School of the Environment, Nanyang Technological University, Singapore

Correspondence
Sarah J. Sapsford
Email: sarah.sapsford@gmail.com

Funding information
New Zealand Ministry of Business, Innovation and Employment; TRY; CONICYT, Grant/Award Number: PIA AFB-170008

Handling Editor: Cyrille Violle

Abstract

1. Biological invasions are a major driver of ecosystem change but causes of variation in their environmental impacts over space and time remain poorly understood. Most approaches used to quantify the impacts of non-native species assume there are interactions among per capita (i.e. individual level) effects, species abundance and the area occupied by the species. However, studies rarely evaluate these factors and their interactions and often fail to recognize that the magnitude of impacts can be highly context dependent. Understanding what drives the context dependence of non-native species impacts can improve our understanding and predictions of ecosystem change and better inform options for mitigation.
2. Conifers, especially pines, are among the most problematic non-native plant species globally. We use Pinaceae to illustrate how context dependence in biodiversity and environmental impacts of non-native plant species can be generated by at least four processes: nonlinear density effects; intraspecific variation in functional traits; shifts in impacts over time; and persistence of impacts as biological or ecosystem legacies following non-native species removal. Using this understanding, we develop a framework to better quantify interactions of impacts along environmental gradients (e.g. soil fertility, climate, ecosystem age).
3. We demonstrate how impacts of non-native species can occur at both low and high density, and that failing to account for intraspecific variation in effect traits can lead to significant errors in the prediction of impacts. By incorporating context dependence in regard to density and functional traits, we can measure how the interaction of this context dependence will shift along environmental gradients.

Moreover, disentangling the roles of species and abundance along such gradients will provide new insights into the net effects of both the native and non-native components of communities. We use a working example of our framework that incorporates all four processes to demonstrate how to measure fire risk impacts of *Pinus contorta*.

4. We show that ecosystem impacts of non-native tree species are not fixed but rather vary predictably along major environmental gradients. Moreover, removal of non-native species through management provides an important tool for revealing biological and ecosystem legacy effects. Although we focus here on relatively well-documented Pinaceae, the new insights into context dependence of impacts can be widely applied across species, environments and regions.

KEYWORDS

belowground legacies, biological invasions, ecological impacts, ecosystem processes, environmental gradients, plant functional traits, plant–soil feedbacks, weeds

1 | INTRODUCTION

Invasions by non-native species result in a wide range of changes to the functioning of ecosystems as well as their provisioning, regulating and cultural services (Castro-Díez et al., 2019; Vilà & Hulme, 2017). Despite rapid growth in quantifying the scale and importance of invasions, the impacts of different non-native species in different systems remain poorly understood (Hulme et al., 2013). Here, we define impact as a positive or negative change in the state of an invaded ecosystem due to a non-native species (Jeschke et al., 2014; Kumschick et al., 2014). We argue that impacts of non-native species are context dependent, with the magnitude and direction of impact contingent on variation in intrinsic (e.g. inter- and intraspecific traits) and extrinsic (e.g. abiotic and biotic environment) factors. Understanding what drives context-dependent non-native species impacts can improve our ability to quantify and predict impacts (Pyšek et al., 2012; Wardle & Peltzer, 2017), which will help optimize management efforts.

Although several frameworks for quantifying the impacts of non-native species have been developed (Thomsen, Olden, Wernberg, Griffin, & Silliman, 2011), the most widely applied framework was defined by Parker et al., (1999). This framework states that impacts (I) depend on the interactions among A, average abundance of the non-native species (measured as number of individuals per m^2), E, effect per individual (i.e. per capita or per-biomass effect) and R, total area occupied by the non-native species (measured as range size in m^2). These are all linked in the formula: $I = A \times E \times R$. We use the term 'density' for abundance throughout this paper as it is per unit area. By including per capita effects or effects per unit biomass, the equation allows biomass-corrected comparisons of the impacts of a given non-native species across different ecosystems or locations, assuming equal effects in all locations. Thus, this framework does not explicitly incorporate context dependence. Ricciardi, Hoopes, Marchetti, and Lockwood (2013) identified the need for addressing the variability of per capita effects and of the interactions of non-native species with their environment, and more recent frameworks (e.g. Kumschick et al., 2014) have addressed the complexity of context dependence that involve interactions among a non-native species, the physicochemical environment and the recipient community. To date, there is no framework that encompasses both of the ideas presented by Ricciardi et al. (2013) and Kumschick et al. (2014).

Here, we propose a comprehensive framework (Figure 1) that demonstrates the context dependence of four variables that need to be incorporated when quantifying impacts of non-native species. We use Pinaceae (and particularly pines) as a case study to explore context dependence of both the density of non-native species and their per capita effects, as well as time since invasion and legacies of non-native species. Furthermore, our framework incorporates the interactions of these context-dependencies across environmental gradients. We focus on ecological, rather than social and economic non-native species impacts since these have been more frequently quantified (Essl et al., 2017).

The Pinaceae are an ideal group for understanding plant invasions (Singh et al., 2018) because they have been widely introduced globally (Essl, Moser, Dullinger, Mang, & Hulme, 2010) and have led to large scale invasions in several regions (Figure 2), where they often cause major ecological impacts (Nuñez et al., 2017). For example, Pinaceae invasions impact water availability (Le Maitre et al., 2002), and can transform landscapes and alter ecosystem function (Dickie et al., 2011). Although we focus primarily on Pinaceae, the principles developed here could potentially be applied to all non-native plant species. We first discuss context dependence through nonlinear density effects, per capita effects, time and legacies. This is followed by a quantitative example of considering multiple context-dependencies and we conclude with a working example of our framework to demonstrate how to measure fire risk impacts of *Pinus contorta*.

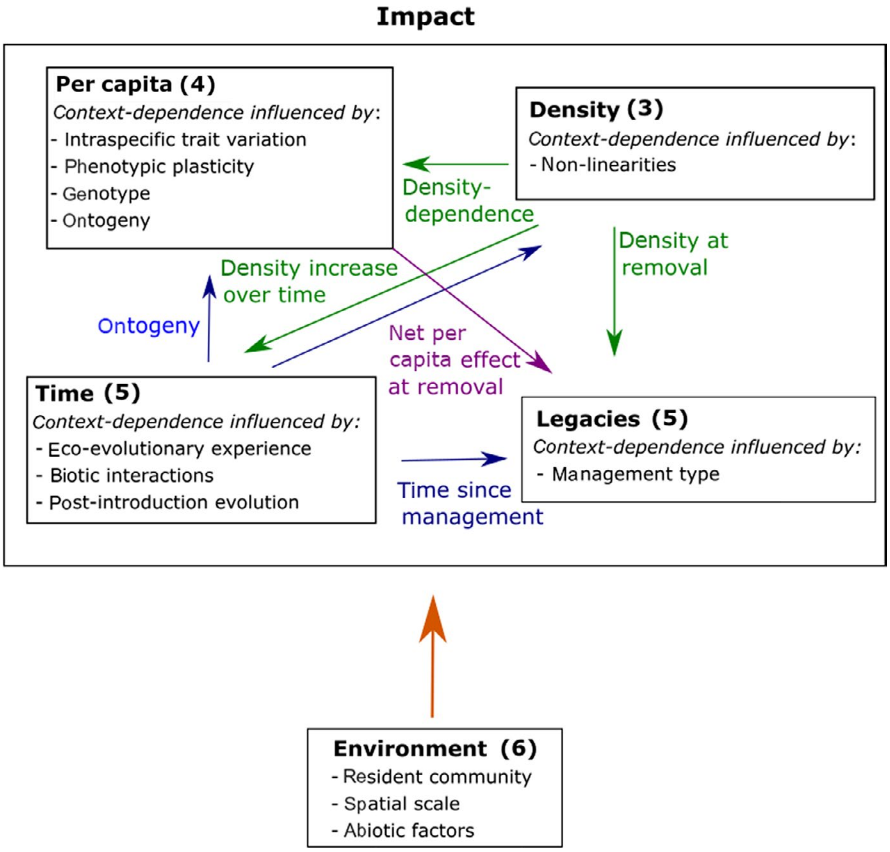

FIGURE 1 Framework for modelling impacts of non-native species along environmental gradients. Impact is defined as a positive or negative change in the state of an invaded ecosystem due to a non-native species. Four variables (i.e. density, per capita, time and legacies) and their sources of context dependence need to be considered when quantifying impacts of non-native species. Environment can influence the direction and strength of the impact. Numbers in parentheses represent the number of the figure in the manuscript where the context dependence of that variable is presented. Arrows indicate direction of influence of one variable on another

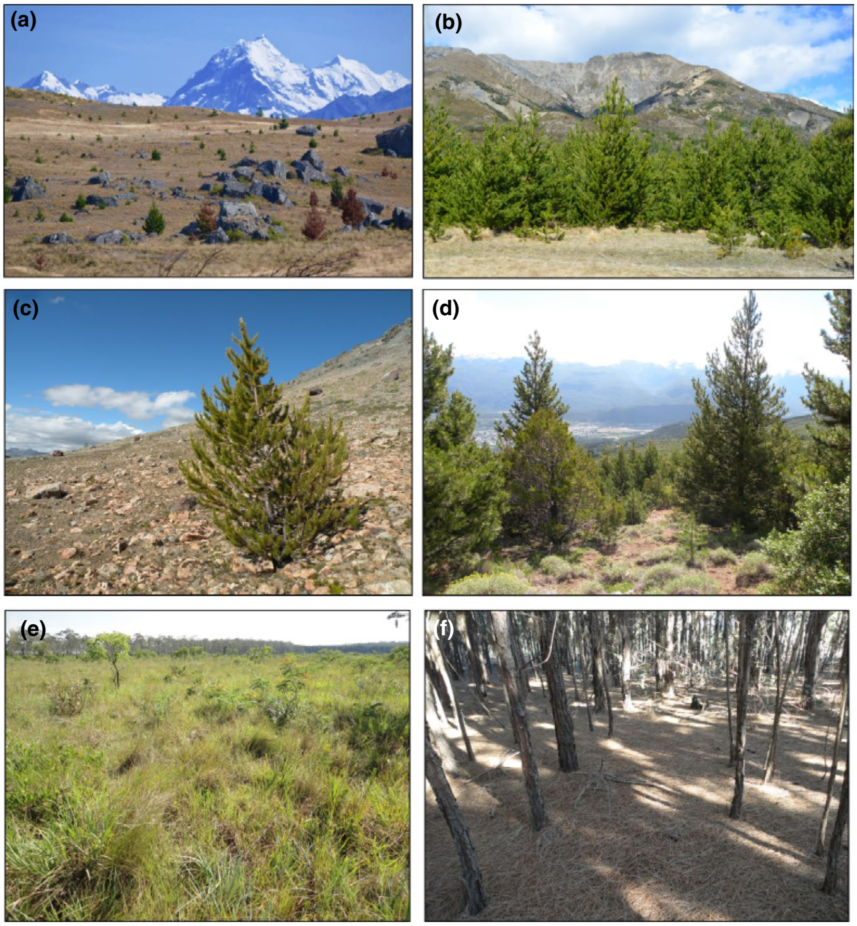

FIGURE 2 Many pine species are native to North America but have been introduced around the world, becoming non-native in many regions in a variety of environments. (a) A young, low density *Pinus contorta* invasion in New Zealand grasslands (Photo: I. A. Dickie). (b) An older, higher density stand of *P. contorta* in New Zealand grasslands (Photo: S. J. Sapsford). (c) An isolated *P. contorta* in Argentina in a high Andean ecosystem (Photo: M. Nuñez). (d) A higher density *P. contorta* invasion in Argentina in a high Andean ecosystem (Photo: M. Nuñez). (e) Uninvaded Brazilian Cerrado ecosystem (Photo: R. Callaway). (f) A Brazilian Cerrado ecosystem invaded by *P. elliotii* (Photo: R. Callaway)

2 | CONTEXT DEPENDENCE

2.1 | Context dependence through nonlinear density effects (*A*)

Impacts of non-native species will be mediated by variation in population density (independent of per capita effects). Non-native species may have impacts on ecosystem function that scale linearly with non-native species density (Figure 3a) or exhibit threshold effects (i.e. nonlinearities) at either low or high density (Bernard-Verdier & Hulme, 2019). Nonlinearities may have critical implications for understanding impacts of non-native species and for the optimal timing of non-native species management (i.e. control or eradication; Panetta & Gooden, 2017). Here we consider evidence for impacts that occur rapidly at low population densities (termed 'low threshold impacts'), at high invasion densities ('high threshold impacts'; Yokomizo, Possingham, Thomas, & Buckley, 2009), or impacts that have a unimodal relationship with density (Figure 3).

Low threshold impacts may be particularly common when impacts are a function of non-native species presence, rather than local abundance (Figure 3b). These impacts are best documented where co-invasion occurs, or multiple-species interactions are involved. For example, pines frequently co-invade with non-native ectomycorrhizal fungi (Nuñez & Dickie, 2014). Once present, these fungi can facilitate the establishment of additional ectomycorrhizal non-native plants. This effect depends on proximity to an established tree rather than tree density, thus mycorrhizal inoculum potential saturates quickly with increasing tree density (Dickie, Schnitzer, Reich, & Hobbie, 2005). Losses of soil carbon and total nitrogen (Figure 3b), increases in labile inorganic phosphorus levels, and declines in soil mite and plant-associated nematode richness all show low threshold impacts (log-linear changes) as a function of *Pinus nigra* density (Dickie et al., 2011). The log-linear response of these variables may reflect the introduction of novel enzymatic pathways due to changes associated with a shift from arbuscular mycorrhizal- to ectomycorrhizal-dominated systems (Nuñez & Dickie, 2014) or changes in quality of litter inputs such as the return of recalcitrant pine needles.

High threshold impacts occur when impacts ensue only once a critical density or biomass is reached (Figure 3c). For example, young or low-density pine invasions do not significantly alter wildfire fuel loads; however, in older or denser invasions, fuel loads and fuel spatial continuity increase rapidly (Figure 3c, where there is a strong increase in total fuel in older invasions), which can result in altered fire behaviour and fire effects (Davis, Maxwell, Caplat, Pauchard, & Nuñez, 2019; Paritsis et al., 2018). High threshold impacts may also occur with litter accumulation, where large amounts of litter bury native vegetation (Brewer, Souza, Callaway, & Durigan, 2018). High threshold impacts can be difficult to predict because they have minimal effect initially; however, these types of impacts occur rapidly once a threshold is crossed which leads to tipping points of rapid

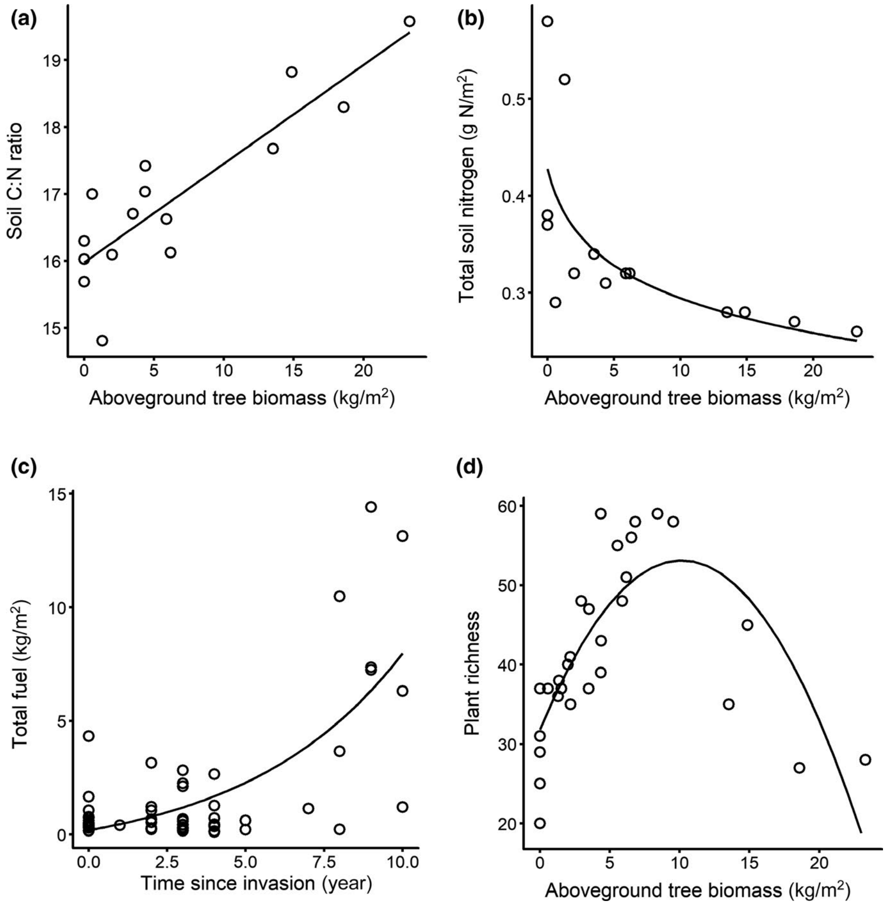

FIGURE 3 Examples of linear and nonlinear impacts of non-native pine species in response to density. (a) A linear response of soil carbon to nitrogen ratio to density of *Pinus nigra* (Dickie et al., 2011). (b) A low threshold response of total soil nitrogen to density of *P. nigra* (Dickie et al., 2011). (c) A high threshold response of total fuel loads to time since invasion of *Pinus contorta* (Taylor et al., 2017). (d) A unimodal response of plant species richness in response to density of *P. nigra* (Dickie et al., 2011)

ecosystem change and potentially high resistance to restoration (Scheffer, Carpenter, Foley, Folke, & Walker, 2001).

In a few cases, unimodal relationships of impacts with pine invasion density have been observed (Figure 3d). An initial increase in plant diversity observed in some invasions (Dickie et al., 2011) may be explained by individual trees ameliorating microclimatic stress, potentially facilitating other plant species and increasing spatial environmental heterogeneity. As pine density increases, however, competition becomes the dominant interaction, resulting in an eventual decline in plant diversity. Although Taylor, Maxwell, Pauchard, Nuñez, and Rew (2016) suggested this decline was linear, a re-analysis of their data supports a unimodal response (albeit lacking an initial increase in diversity; see Appendix S1, Figure S1). Other unimodal responses could be those linked to leaf area index (LAI) of the non-native species: LAI shows a strong linear increase at very low densities of pine but declines precipitously once tree canopies begin to overlap, reflecting predictable shifts in canopy development and form from sparse open-canopy to closed-canopy stands (Dickie et al., 2011).

2.2 | Context dependence in per capita effects (*E*)

Per capita effect, or the effect size per individual, is mediated by the effect traits of the species in question (Hulme et al., 2013; Ricciardi et al., 2013; Suding et al., 2008) and intraspecific variation in those traits. Plant traits typically fall along two main axes: one reflecting a trade-off between species height, stem specific density and seed size and the other describing whether a species has an exploitative (nitrogen-rich, short-lived tissues) or conservative (nitrogen-poor, long-lived tissues) resource use strategy (Díaz et al., 2016). These traits are strongly linked to the effect of species on ecosystem properties. For example, variation in traits related to resource use strategy (e.g. specific leaf area [SLA] and leaf nitrogen [N] concentration) strongly determines rates of litter decomposition (Cornwell et al., 2008), and variation in stem density affects carbon storage, hydrological functions (Matheny, Mirfenderesgi, & Bohrer, 2017) and tree flammability (Frejaville, Curt, & Carcaillet, 2013).

The quantification of per capita effects typically assumes that an individual's effect will be the same regardless of context. Because of this, the traits used to assess ecological impacts have traditionally focused on species level variation. However, substantive intraspecific variation has been found for many traits (Hulme & Bernard-Verdier, 2018). For example, variation in SLA, leaf N concentration and wood density of 30 Pinaceae across seven genera can be an order of magnitude greater within species than among species or genera (Figure 4a; Appendix S2 for methods; Kattge et al., 2011). Moreover, for some species this intraspecific variation encompasses a significant proportion of the global range of these traits (Figure 4b; Figure S2; Pérez-Harguindeguy et al., 2013). This is the case for *Pinus halepensis* and highlights that such high levels of variation within species should translate to significant variation in impacts (Pyšek et al., 2012; Wardle, Bardgett, Callaway, & Van der Putten, 2011). A lack of consideration of intraspecific trait variation when quantifying impacts could therefore lead to significant errors. For example, wood density is multiplied by stem volume to provide an estimate of aboveground carbon storage. Based on the over twofold difference in density observed in *P. halepensis* and *Pinus sylvestris* (Figure 4b), the actual carbon storage in a system could range from 54% lower to 31% higher than estimates calculated using these species' mean wood density values.

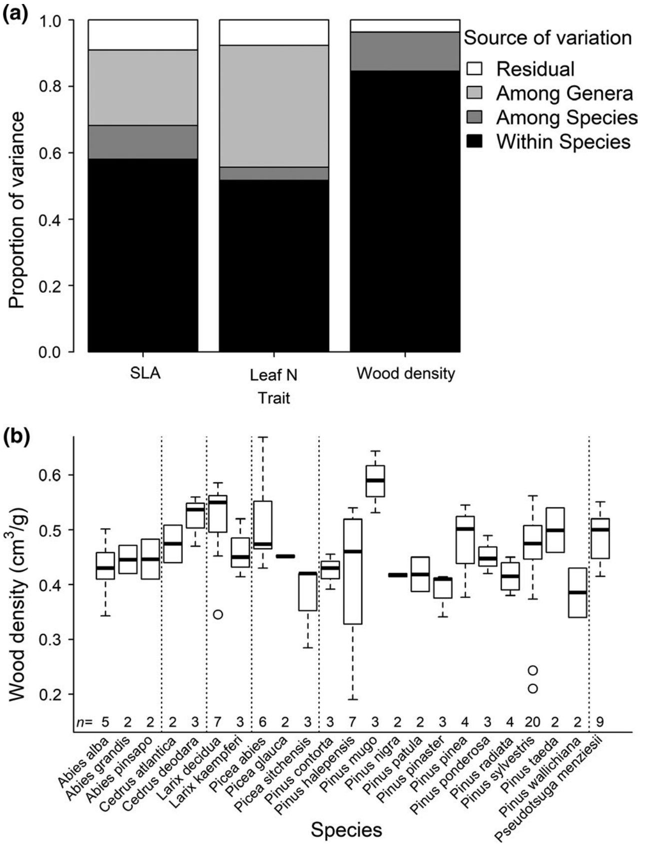

FIGURE 4 Intraspecific variation in plant traits. (a) Proportion of variance in specific leaf area (SLA), leaf nitrogen (N) concentration, and wood density of non-native Pinaceae explained by genus, species within genus and observations within species, plus residual error. (b) Variation in wood density illustrated for 23 species across 6 genera. For each boxplot, the median value is represented by a horizontal line, the first and third quartiles by boxes and values outside the quartiles by whiskers. Outliers are values >1.5 times the interquartile range. Data for (a) and (b) are from the TRY database and associated references; see Table S2.1 (*n* = 99 observations in total). For (b), each focal species in these six genera is non-native in at least two global regions (Essl et al., 2010; see Table S2.1 for the complete species list)

Variation in plant functional traits can be driven by species density, genetic, ontogenetic and environmental factors (e.g. soil fertility, water availability). For example, tree density has been shown to modify productivity, transpiration rates and water use efficiency (Eastham, Rose, Charles-Edwards, Cameron, & Rance, 1990). The extent to which such intraspecific variation reflects genotype or environment interactions remains unclear, but progeny trials using *Pinus* species confirm that several traits, including wood density

(Lin et al., 2014) and leaf N concentration (Reich, Oleksyn, & Tjoelker, 1996), have a strong genetic component at the within-species level. Different genotypes of the same species of *Pinus* might therefore have quite different effects even in similar environments. The variability of observed impacts across a species' introduced range may also increase due to genotype by environment interactions that amplify intraspecific trait variation and can lead it to increase over time. Understanding both the drivers and consequences of trait variation within non-native species (and thereby, potentially, their per capita effect) may therefore enable more accurate predictions of their impacts in new sites and on the communities to which they are introduced.

2.3 | Context dependence in time

Time is an important driver of context dependence (Figure 1) through its influence on non-native species biomass, density and age (and thus per capita effects), as well as on changes in biotic and abiotic variables (Strayer, Eviner, Jeschke, & Pace, 2006) and, in the longer term, evolution. Invasion impact trajectories over time can be predictable, with an acute phase of impacts that occur immediately or shortly after non-native species arrival followed by a chronic or lag phase that occurs after ecological and evolutionary processes have progressed (Strayer et al., 2006). The main challenge with discerning time-related context dependence is that most studies are either short-term (<5 years duration) or conducted well after the initial invasion started (≥50 years post-invasion; D'Antonio & Flory, 2017). Space-for-time substitutions (comparison of invaded to uninvaded sites) can overcome this challenge, in part. However, combining a time approach (pre- vs. post-invasion comparisons) with a space-for-time substitution can more accurately predict non-native species impacts (see framework by Thomaz et al., 2012; and experimental design proposed by Kumschick et al., 2014).

Biotic and abiotic interactions formed over the time of an invasion can influence impacts of non-native species. Pathogen accumulation on non-native species over time may reduce non-native plant fitness (Diez et al., 2010), whereas increasing the risk of pathogen spill-over or spill-back (Dickie et al., 2017). Such negative plant–soil feedbacks may reverse initial negative impacts of a non-native species on native species and result in coexistence between native and non-native plant species (Dostál, Müllerová, Pyšek, Pergl, & Klinerová, 2013). Similarly, inputs of non-native species to soil chemical and organic pools may accumulate over time. Pine invasions into grasslands are associated with initial losses of soil carbon pools (Chapela, Osher, Horton, & Henn, 2001). Over time, the continual input of pine litter to these soils is likely to increase carbon pools, leading to high organic matter soils typically associated with pine in its native range. Similarly, soil pH under *Pinus radiata* shows a gradual decrease with time (estimated at 0.3 units/year over 11 years; Parfitt & Ross, 2011), potentially leading to threshold responses of soil nutrient availability and biota.

Pre-introduction evolutionary history, such as eco-evolutionary experience, can play a major role in impacts of non-native species during the acute phase of invasion (Zenni, Dickie, et al., 2017). For example, greater impacts are seen in regions where there are no native equivalents of the invading non-native species (Davis, Callaway, et al., 2019). As such, non-native *P. contorta* has greater impacts in the Southern Hemisphere where there are no native *Pinus* spp. compared to its impact in the Northern Hemisphere where other *Pinus* spp. do occur (Davis, Callaway, et al., 2019).

In later phases of an invasion, post-introduction evolution can contribute to an increase in a plant's impact and alter evolutionary responses of native species through a variety of processes including local adaptation, drift and phenotypic plasticity (Zenni, Dickie, et al., 2017). For a native species, such processes allow species to adapt in response to an invasion (Hulme & Le Roux, 2016). For a non-native species, such processes contribute to local adaptation and range expansion (Colautti & Barrett, 2013). For example, evolutionary changes (through the process of rapid evolution) in plant growth rate and leaf traits in non-native *Pinus taeda* have been shown to be correlated with greater rates of its spread just 40 years after its introduction to southern Brazil (Zenni, Cunha, & Sena, 2016). Being aware of these various mechanisms of context dependence in time and implementing both time and space-for-time approaches are important for improving predictions of non-native species impacts.

2.4 | Legacies

We define legacies as effects of non-native species that remain after the species has been removed through changes in soil biological, chemical or physical conditions and subsequent plant communities (Corbin & D'Antonio, 2012). Legacies can be difficult to reverse and can make restoration of an ecosystem difficult or unattainable (Wardle & Peltzer, 2017). The context-dependent nature of legacy effects is often related to non-native species density and net per capita effect at the time of removal (Figure 1). Management involving removal of the invader also has the potential to influence legacy effects via non-target impacts of the removal method (e.g. via clear felling, fire or herbicide sprays for non-native pines).

By incorporating density, per capita and time effects, we can determine if and how long legacy effects remain after non-native species removal (Figure 5). At any point in time, impacts of a non-native species may increase or decrease as a function of density and per capita effects (see quantitative example in Section 3.1). Impacts can have nonlinear responses to density, and density at the time of removal (i.e. management in Figure 5) is therefore an important determinant of the context dependence of legacy effects. This might be especially important for low threshold impacts such as losses of soil carbon and total nitrogen (Figure 3b; Dickie et al., 2011), which might thus translate into legacy effects even if removal is undertaken at relatively low densities. In other cases, early removal of small, sparse individuals may limit legacies because there is little opportunity for the

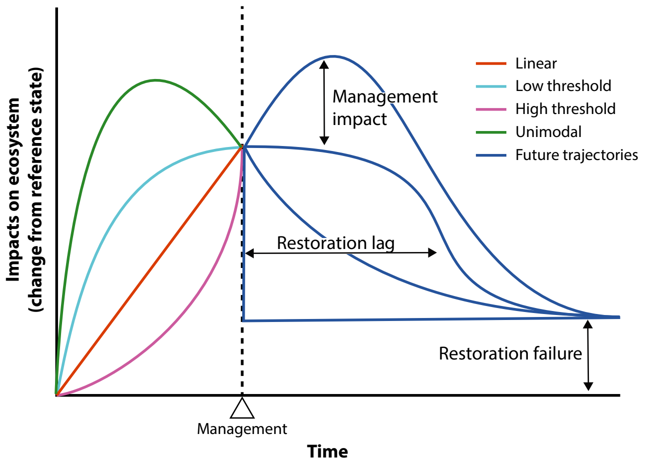

FIGURE 5 Theoretical effects of management on legacies: over a period of time, impacts (change from a reference state) of non-native species within an ecosystem may increase or decrease as a function of impact-associated traits, population density and environment. Specifically, nonlinear effects of density can occur where an impact demonstrates a unimodal response to density (given the assumption that density will increase over time), a low threshold response, a linear response or a high threshold response. At some point, management is applied which could result in various trajectories. The effects of removal may not be observed immediately and thus there may be a restoration lag. Depending on the management type used, management itself may have an impact (i.e. management-specific legacies). Management may also fail to fully remove impacts, resulting in partial or complete restoration failure (i.e. difference measured from reference state [black horizontal axis]). How these different legacy scenarios relate to pre-management density/impact trajectories remains unknown

species to impact the ecosystem irrespective of their per capita effects (Dickie et al., 2014). In contrast, older and larger established invasions can impact ecosystems by replacing communities of native plant species, insects and birds (Daniel & Williams, 1984; Howell & McAlpine, 2016). As depicted in Figure 5, after management, we may see a restoration lag, where dissipation of a non-native species' impact and subsequent ecosystem restoration requires a certain period of time. However, in many cases where legacies exist, restoration fails (i.e. due to a change from a reference state; Figure 5).

The method of non-native species removal can also have unintended or deleterious outcomes resulting in management impacts (Figure 5). Management of non-native pines spans a range of spatial scales and intensities from the mechanical removal of small individuals through to relatively large-scale application of non-selective herbicides (Nuñez et al., 2017). Management of large individual trees or closed-canopy stands can involve clear felling, which rapidly alters the abundance of the non-native species. In these large-scale management practices, most native vegetation is also removed. This may result in a management impact that increases the impact of a non-native species on an ecosystem, possibly lengthening the restoration lag and increasing the likelihood of restoration failure (Figure 5). Additional restoration or secondary management for reestablishment of native communities may be required. For example, following *P. contorta* removal, native seedling establishment has been shown to be higher in areas where seeds were sown in comparison to those where seeds were not added (McAlpine, Howell, & Wotton, 2016). In some cases, removal of one non-native species is followed directly by invasion of others. Such secondary invasions are widespread (Corbin & D'Antonio, 2012), and some evidence suggests that removal of non-native pines can facilitate secondary invasion by grasses or other woody non-native species (Dickie et al., 2014). Knowledge of management legacies is thus an important aspect of the context dependence of non-native species impacts and is critical for informing decisions on both management effectiveness in mitigating invasion impacts, and on whether additional activities such as active restoration following removal of the non-native species are needed (Wardle & Peltzer, 2017).

3 | MULTIPLE CONTEXT-DEPENDENCIES

3.1 | Quantitative example

The 'total' impact of a non-native species can be quantified by combining density, per capita, time and legacy effects and accounting for their context dependencies (Figure 1). Impact can also be expressed as a change from a reference state (Figure 5) and vary along environmental gradients (e.g. soil fertility, climate, ecosystem age). For simplicity, we provide a quantitative example of measuring non-native species impacts along an environmental gradient as the product of two variables within our framework: density and per capita effects (Figure 6; see Kardol, Fanin, & Wardle, 2018 for an empirical example; Appendix S3 for quantitaive methodology).

The impact of a species as a product of density (number of individuals) and per capita (effect of each individual) can vary across an environmental gradient. Shifts in the density of individual species along environmental gradients is relatively easily characterized and well-studied (Lomolino, 2001). In contrast, the influence of environmental factors on per capita effects is less well understood, but recent studies demonstrate that species' effects vary among ecosystems (e.g. Isbell et al., 2017). For example, as ecosystem productivity increases, individual trees can increase their height and allocate relatively more biomass to wood, thus returning less leaf and fine root litter to the ecosystem per unit biomass (e.g. Poorter, Lianes, Moreno-de las Heras, & Zavala, 2012). Here we have assumed, for simplicity, that both density and per capita effects follow a normal distribution along a gradient (Figure 6a; Appendix S3). In our example, maximum tree density is derived empirically from a *P. nigra* invasion in New Zealand (Dickie et al., 2011), and corresponds to *c.* 4 trees (>2.5 cm diameter at 1.35 m height) per m^2 (Figure 6a). Impacts mediated by density do not necessarily scale linearly; as we discussed in Section 2.1, some impacts can display either low and high threshold responses or unimodal responses (Figure 6b; Appendix S3). Similarly, the height of the per capita curve changes

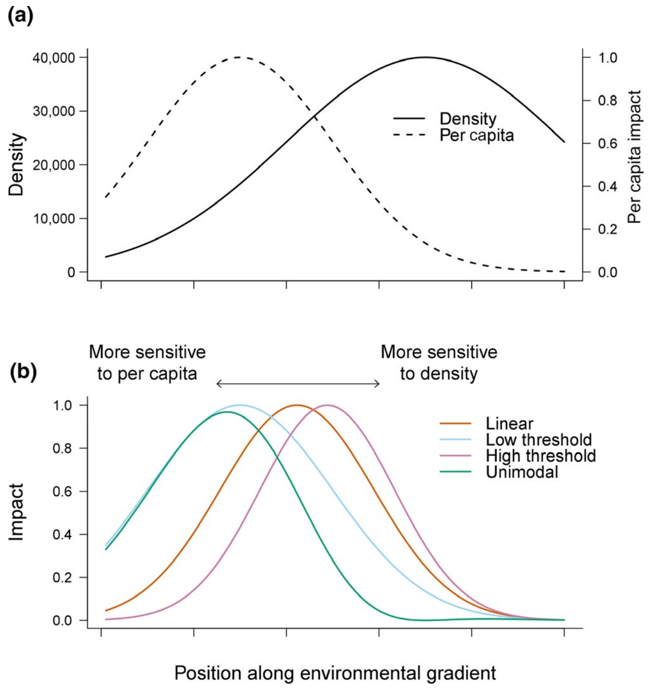

FIGURE 6 Quantifying impacts of non-native species as a function of density (number of individuals per m^2) and per capita effects (effect per individual) across an environmental gradient. (a) Both the density (max = 4 trees/m^2) of a species and its per capita effects (proportion of maximum) can vary along environmental gradients. Common gradients include stand age or stage of development, elevation, soil fertility or ecosystem age. (b) Net impacts of a species across the gradient for each of four varying responses (linear, low threshold, high threshold and unimodal) to density of a non-native species (see Figure 2), displayed as different coloured functions. At each position along the gradient, the impact is a product of density and per capita effect (see Appendix S3 for methods)

along the environmental gradient because species trait expression changes along the gradient (Figure 6b; due to factors discussed in Section 2.2). Whether the magnitude or importance of intraspecific trait variation shifts predictably along environmental gradients is little understood. Exploring trait variation along environmental gradients will be necessary in confirming the importance of this variable in predicting impacts of non-native species.

To measure impact (density × per capita) for a non-native species in the field, we can quantify the mean per capita effects of a species on a response variable (Dickie et al., 2011) and multiply that by the population density to generate the impact for that position along an environmental gradient. Removal experiments can be used to generate a reference state (Peltzer et al., 2009), whereby the difference in a response variable between the invaded and non-invaded treatments can be used to quantify impact; these types of experiments would also incorporate legacy effects. Such experiments can be replicated along an environmental gradient to compare impacts along the gradient, as shown by Kardol et al. (2018) and Fanin et al. (2019). These experimental approaches can also be applied to multiple species along a gradient. One potential complication of this approach is that synergistic or antagonistic interactions among species may occur rather than simply additive effects. However, removal experiments have been shown to be successful in comparing the impact of three coexisting species, and of interactive effects among these three species on a suite of ecosystem properties along an environmental gradient (Kardol et al., 2018). Furthermore, differences in impacts along environmental gradients can elucidate the level of biotic resistance of communities of non-native species.

3.2 | Working example of framework: Increased fire risk

One of the most problematic and widespread non-native pine species, *P. contorta*, has been shown to alter fuel loads and structure, which is likely to increase fire spread and severity (Cóbar-Carranza, García, Pauchard, & Peña, 2014; Paritsis et al., 2018; Taylor et al., 2017). Specifically, *P. contorta* may also increase landscape flammability through differences from native tree species in key functional traits such as foliar moisture content (ignitability), crown bulk density (sustainability), heat and volatile content (combustibility) and fine fuel proportion (consumability; Cóbar-Carranza et al., 2014). Taking these specific functional traits into consideration, we work through an example of how the four variables in the framework presented in Figure 1 (i.e. density, per capita, time and legacies) could be applied to assess the impact of increased fire risk from a non-native species.

First, total fuel loads demonstrate a nonlinear response to time since invasion of *P. contorta*: as *P. contorta* invasions age and become more dense, the total fuel load increases, and this has been observed in invaded regions in Chile, Argentina and New Zealand (high threshold response Figures 1 and 3c; Taylor et al., 2017). Second, functional traits that drive flammability and crown fire potential also have key context dependencies. Crown bulk density varies with stand density and across sites (Reinhardt, Scott, Gray, & Keane, 2006), whereas foliar moisture content and heat content can vary over time (Figure 1; Qi, Jolly, Dennison, & Kropp, 2016). Third, legacies of *P. contorta* can also affect fire risk: if individuals are felled but not removed from the area, a large amount of biomass (and thus fuel) remains close to the soil surface where it can increase soil heating and cause stronger fire effects on native vegetation (management impacts in Figures 1 and 5; Holmes, Richardson, Van Wilgen, & Gelderblom, 2000; Taylor et al., 2017). In comparison, if felled trees are removed, the fire risk is greatly reduced. The effects of time can influence density, per capita and legacy effects.

Lastly, the environment into which these trees are invading can influence the impact of *P. contorta* on fire risk (Figures 1 and 6). If the environment spans an area from wet to arid, one would expect individuals within the arid zone may pose a greater threat by contributing fuel to a fuel-limited system (Krawchuk & Moritz, 2011). Similarly, the surrounding resident community could also increase or decrease the magnitude of the impact. For example, if *P. contorta* invades a resident community with low canopy bulk density or higher foliar moisture, fire risk may be low, especially at early stages of invasion (Cóbar-Carranza et al., 2014). By taking all the components of the framework (i.e. density, per capita, time and legacies) into consideration, it would be possible to accurately predict the impact *P. contorta* has on fire risk in a community, ecosystem or region. By taking a similar approach as above, this framework can be applied to other non-native species by measuring each variable within our framework for the species in question.

4 | FUTURE DIRECTIONS

We have demonstrated that impacts of non-native plant species on ecosystems are highly context dependent through nonlinear responses to density, intraspecific variation in per capita effects and temporal legacies. By including these context dependencies, we have developed a framework to model impacts of non-native species across environmental gradients. However, we suggest several further directions that stem from our proposed framework and that will serve to further improve predictions of non-native species impacts.

First, the extent to which our framework can be extrapolated to other non-native taxa (such as other plant species but also animals) that occupy a range of environmental conditions or that occur across broad environmental gradients needs to be explored. Second, there is a need to apply this framework to a broader (e.g. global) scale. As many non-native species occur over broad geographic ranges (Seebens et al., 2018), comparing a species' impacts across regions or continents would inform predictions of its impacts over these larger scales. For example, non-native pines have been shown to shift towards faster growth rates, greater reproductive efforts and higher rates of establishment in their introduced compared to native ranges (Davis, Callaway, et al., 2019). Third, there is a need to determine if our framework can be used in conjunction with other species data to predict future impacts of newly arrived or potential invaders. Fourth, it is important to determine whether the context dependence of a non-native species impacts in its native range can suggest its likely impacts in its invaded range (Kumschick et al., 2014). Finally, in some cases multiple species simultaneously invade an area, and it is therefore necessary to better understand the extent to which impacts from multiple non-native species are additive versus synergistic.

Furthermore, a focus is needed on the effects of time, relationships with antagonists and mutualists and legacies on the impacts of non-native species to improve our ability to predict the consequences of different types of context dependence on non-native species impacts. Taking such variables into consideration is critical for refining decisions on both management effectiveness in mitigating invasion impacts, and whether additional activities such as active restoration following non-native species control are needed to achieve desired outcomes. Through this work, we will be better placed to identify critical points or tipping points resulting from an invasion and act before recovery of an ecosystem becomes unattainable.

ACKNOWLEDGEMENTS

We thank Flock Hill Station for providing an excellent venue and services for the workshop that led to this paper, L. Gillanders for assistance with logistics and the New Zealand Ministry of Business, Innovation and Employment for financial support through the Winning Against Wildings research programme. This study has been supported by the TRY initiative on plant traits (http://www.try-db.org). The TRY initiative and database is hosted, developed and maintained by J. Kattge and G. Boenisch (Max Planck Institute for Biogeochemistry, Jena, Germany). TRY is currently supported by Future Earth/bioDISCOVERY and the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig. AP funded by CONICYT PIA AFB-170008. We thank three anonymous reviewers whose comments greatly improved the paper.

AUTHORS' CONTRIBUTIONS

All authors contributed substantially to the development of this manuscript throughout a dedicated workshop on 'Wilding conifer impacts and legacies'. D.A.P. organised the workshop, D.A.P., I.A.D. and P.E.H. designed the original outline of the paper, and S.J.S. completed the manuscript with inputs from all authors.

DATA AVAILABILITY STATEMENT

Data are publicly available in the Manaaki Whenua Landcare Research DataStore https://doi.org/10.7931/bmpy-ad80 (Brandt, 2020). https://datastore.landcareresearch.co.nz/dataset/invasive-pinaceae-traits-2018.

ORCID

Sarah J. Sapsford https://orcid.org/0000-0001-6019-5063
Angela J. Brandt https://orcid.org/0000-0001-5980-9128
Kimberley T. Davis https://orcid.org/0000-0001-9727-374X
Guadalupe Peralta https://orcid.org/0000-0003-1947-4989
Ian A. Dickie https://orcid.org/0000-0002-2740-2128
Philip E. Hulme https://orcid.org/0000-0001-5712-0474
Martin A. Nuñez https://orcid.org/0000-0003-0324-5479
Kate H. Orwin https://orcid.org/0000-0003-0906-728X
Anibal Pauchard https://orcid.org/0000-0003-1284-3163
David A. Wardle https://orcid.org/0000-0002-0476-7335
Duane A. Peltzer https://orcid.org/0000-0001-7724-3738

REFERENCES

Bernard-Verdier, M., & Hulme, P. E. (2019). Alien plants can be associated with a decrease in local and regional native richness even when at low abundance. *Journal of Ecology*, *107*(3), 1343–1354. https://doi.org/10.1111/1365-2745.13124

Brandt, A. J. (2020). Data from: Invasive Pinaceae traits 2018. *DataStore: The Manaaki Whenua-Landcare Research Data Repository*, https://doi.org/10.7931/bmpy-ad80

Brewer, J. S., Souza, F. M., Callaway, R. M., & Durigan, G. (2018). Impact of invasive slash pine (*Pinus elliottii*) on groundcover vegetation at home and abroad. *Biological Invasions*, *20*(10), 2807–2820. https://doi.org/10.1007/s10530-018-1734-z

Castro-Díez, P., Vaz, A. S., Silva, J. S., Loo, M., Alonso, Á., Aponte, C., … Godoy, O. (2019). Global effects of non-native tree species on multiple ecosystem services. *Biological Reviews*, *94*(4), 1477–1501. https://doi.org/10.1111/brv.12511

Chapela, I. H., Osher, L. J., Horton, T. R., & Henn, M. R. (2001). Ectomycorrhizal fungi introduced with exotic pine plantations induce soil carbon depletion. *Soil Biology and Biochemistry*, *33*(12), 1733–1740. https://doi.org/10.1016/S0038-0717(01)00098-0

Cóbar-Carranza, A. J., García, R. A., Pauchard, A., & Peña, E. (2014). Effect of *Pinus contorta* invasion on forest fuel properties and its potential implications on the fire regime of *Araucaria araucana* and *Nothofagus antarctica* forests. *Biological Invasions*, *16*(11), 2273–2291. https://doi.org/10.1007/s10530-014-0663-8

Colautti, R. I., & Barrett, S. C. H. (2013). Rapid adaptation to climate facilitates range expansion of an invasive plant. *Science*, *342*(6156), 364–366. https://doi.org/10.1126/science.1242121

Corbin, J. D., & D'Antonio, C. M. (2012). Gone but not forgotten? Invasive plants' legacies on community and ecosystem properties. *Invasive Plant Science and Management*, *5*(1), 117–124. https://doi.org/10.1614/IPSM-D-11-00005.1

Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., … Westoby, M. (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, *11*(10), 1065–1071. https://doi.org/10.1111/j.1461-0248.2008.01219.x

Daniel, M. J., & Williams, G. R. (1984). A survey of the distribution, seasonal activity and roost sites of New Zealand bats. *New Zealand Journal of Ecology*, *7*, 9–25.

D'Antonio, C., & Flory, S. L. (2017). Long-term dynamics and impacts of plant invasions. *Journal of Ecology*, *105*(6), 1459–1461. https://doi.org/10.1111/1365-2745.12879

Davis, K. T., Callaway, R. M., Fajardo, A., Pauchard, A., Nuñez, M. A., Brooker, R. W., … Gundale, M. J. (2019). Severity of impacts of an introduced species corresponds with regional eco-evolutionary experience. *Ecography*, *42*(1), 12–22. https://doi.org/10.1111/ecog.04014

Davis, K. T., Maxwell, B. D., Caplat, P., Pauchard, A., & Nuñez, M. A. (2019). Simulation model suggests that fire promotes lodgepole pine (*Pinus contorta*) invasion in Patagonia. *Biological Invasions*, *21*(7), 2287–2300. https://doi.org/10.1007/s10530-019-01975-1

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., … Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, *529*, 167. https://doi.org/10.1038/nature16489

Dickie, I. A., Bufford, J. L., Cobb, R. C., Desprez-Loustau, M.-L., Grelet, G., Hulme, P. E., … Williams, N. M. (2017). The emerging science of linked plant–fungal invasions. *New Phytologist*, *215*(4), 1314–1332. https://doi.org/10.1111/nph.14657

Dickie, I. A., Schnitzer, S. A., Reich, P. B., & Hobbie, S. E. (2005). Spatially disjunct effects of co-occurring competition and facilitation. *Ecology Letters*, *8*(11), 1191–1200. https://doi.org/10.1111/j.1461-0248.2005.00822.x

Dickie, I. A., St John, M. G., Yeates, G. W., Morse, C. W., Bonner, K. I., Orwin, K., & Peltzer, D. A. (2014). Belowground legacies of *Pinus contorta* invasion and removal result in multiple mechanisms of invasional meltdown. *AoB PLANTS*, *6*, 1–15. https://doi.org/10.1093/aobpla/plu056

Dickie, I. A., Yeates, G. W., St. John, M. G., Stevenson, B. A., Scott, J. T., Rillig, M. C., … Aislabie, J. (2011). Ecosystem service and biodiversity trade-offs in two woody successions. *Journal of Applied Ecology*, *48*(4), 926–934. https://doi.org/10.1111/j.1365-2664.2011.01980.x

Diez, J. M., Dickie, I., Edwards, G., Hulme, P. E., Sullivan, J. J., & Duncan, R. P. (2010). Negative soil feedbacks accumulate over time for non-native plant species. *Ecology Letters*, *13*(7), 803–809. https://doi.org/10.1111/j.1461-0248.2010.01474.x

Dostál, P., Müllerová, J., Pyšek, P., Pergl, J., & Klinerová, T. (2013). The impact of an invasive plant changes over time. *Ecology Letters*, *16*(10), 1277–1284. https://doi.org/10.1111/ele.12166

Eastham, J., Rose, C., Charles-Edwards, D., Cameron, D., & Rance, S. (1990). Planting density effects on water use efficiency of trees and pasture in an agroforestry experiment. *New Zealand Journal of Forestry Science*, *20*(1), 39–53.

Essl, F., Hulme, P. E., Jeschke, J. M., Keller, R., Pyšek, P., Richardson, D. M., … Rabitsch, W. (2017). Scientific and normative foundations for the valuation of alien-species impacts: Thirteen core principles. *BioScience*, *67*(2), 166–178. https://doi.org/10.1093/biosci/biw160

Essl, F., Moser, D., Dullinger, S., Mang, T., & Hulme, P. E. (2010). Selection for commercial forestry determines global patterns of alien conifer invasions. *Diversity and Distributions*, *16*(6), 911–921. https://doi.org/10.1111/j.1472-4642.2010.00705.x

Fanin, N., Kardol, P., Farrell, M., Kempel, A., Ciobanu, M., Nilsson, M.-C., … Wardle, D. A. (2019). Effects of plant functional group removal on structure and function of soil communities across contrasting ecosystems. *Ecology Letters*, *22*(7), 1095–1103. https://doi.org/10.1111/ele.13266

Frejaville, T., Curt, T., & Carcaillet, C. (2013). Bark flammability as a fire-response trait for subalpine trees. *Frontiers in Plant Science*, *4*. https://doi.org/10.3389/fpls.2013.00466

Holmes, P. M., Richardson, D. M., Van Wilgen, B. W., & Gelderblom, C. (2000). Recovery of South African fynbos vegetation following alien woody plant clearing and fire: Implications for restoration. *Austral Ecology*, *25*(6), 631–639. https://doi.org/10.1111/j.1442-9993.2000.tb00069.x

Howell, C. J., & McAlpine, K. G. (2016). Native plant species richness in non-native *Pinus contorta* forest. *New Zealand Journal of Ecology*, *40*(1), 131–136. https://doi.org/10.20417/nzjecol.40.15

Hulme, P. E., & Bernard-Verdier, M. (2018). Comparing traits of native and alien plants: Can we do better? *Functional Ecology*, *32*(1), 117–125. https://doi.org/10.1111/1365-2435.12982

Hulme, P. E., & Le Roux, J. J. (2016). Invasive species shape evolution. *Science*, *352*(6284), 422. https://doi.org/10.1126/science.352.6284.422-b

Hulme, P. E., Pyšek, P., Jarošík, V., Pergl, J., Schaffner, U., & Vilà, M. (2013). Bias and error in understanding plant invasion impacts. *Trends in Ecology & Evolution*, *28*(4), 212–218. https://doi.org/10.1016/j.tree.2012.10.010

Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Díaz, S., Hector, A., … Larigauderie, A. (2017). Linking the influence and dependence of people on biodiversity across scales. *Nature*, *546*, 65. https://doi.org/10.1038/nature22899

Jeschke, J. M., Bacher, S., Blackburn, T. M., Dick, J. T. A., Essl, F., Evans, T., … Kumschick, S. (2014). Defining the impact of non-native species. *Conservation Biology*, *28*(5), 1188–1194. https://doi.org/10.1111/cobi.12299

Kardol, P., Fanin, N., & Wardle, D. A. (2018). Long-term effects of species loss on community properties across contrasting ecosystems. *Nature*, *557*(7707), 710–713. https://doi.org/10.1038/s41586-018-0138-7

Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., … Wirth, C. (2011). TRY – A global database of plant traits. *Global Change Biology*, *17*(9), 2905–2935. https://doi.org/10.1111/j.1365-2486.2011.02451.x

Krawchuk, M. A., & Moritz, M. A. (2011). Constraints on global fire activity vary across a resource gradient. *Ecology*, *92*(1), 121–132. https://doi.org/10.1890/09-1843.1

Kumschick, S., Gaertner, M., Vilà, M., Essl, F., Jeschke, J. M., Pyšek, P., … Winter, M. (2014). Ecological impacts of alien species: Quantification, scope, caveats, and recommendations. *BioScience*, *65*(1), 55–63. https://doi.org/10.1093/biosci/biu193

Le Maitre, D. C., van Wilgen, B. W., Gelderblom, C. M., Bailey, C., Chapman, R. A., & Nel, J. A. (2002). Invasive alien trees and water resources in South Africa: Case studies of the costs and benefits of management. *Forest Ecology and Management*, *160*(1), 143–159. https://doi.org/10.1016/S0378-1127(01)00474-1

Lin, Y., Yang, H., Ivković, M., Gapare, W. J., Matheson, A. C., & Wu, H. X. (2014). Effect of genotype-by-spacing interaction on radiata pine wood density. *Australian Forestry*, *77*(3–4), 203–211. https://doi.org/10.1080/00049158.2014.980878

Lomolino, M. V. (2001). Elevation gradients of species-density: Historical and prospective views. *Global Ecology and Biogeography*, *10*(1), 3–13. https://doi.org/10.1046/j.1466-822x.2001.00229.x

Matheny, A. M., Mirfenderesgi, G., & Bohrer, G. (2017). Trait-based representation of hydrological functional properties of plants in weather and ecosystem models. *Plant Diversity*, *39*(1), 1–12. https://doi.org/10.1016/j.pld.2016.10.001

McAlpine, K. G., Howell, C. J., & Wotton, D. M. (2016). Effects of tree control method, seed addition, and introduced mammal exclusion on seedling establishment in an invasive *Pinus contorta* forest. *New Zealand Journal of Ecology*, *40*(3), 302–309. https://doi.org/10.20417/nzjecol.40.32

Nuñez, M. A., Chiuffo, M. C., Torres, A., Paul, T., Dimarco, R. D., Raal, P., … Richardson, D. M. (2017). Ecology and management of invasive Pinaceae around the world: Progress and challenges. *Biological Invasions*, *19*(11), 3099–3120. https://doi.org/10.1007/s10530-017-1483-4

Nuñez, M. A., & Dickie, I. A. (2014). Invasive belowground mutualists of woody plants. *Biological Invasions*, *16*(3), 645–661. https://doi.org/10.1007/s10530-013-0612-y

Panetta, F. D., & Gooden, B. (2017). Managing for biodiversity: Impact and action thresholds for invasive plants in natural ecosystems. *NeoBiota*, *34*, 53–66. https://doi.org/10.3897/neobiota.34.11821

Parfitt, R. L., & Ross, D. J. (2011). Long-term effects of afforestation with *Pinus radiata* on soil carbon, nitrogen, and pH: A case study. *Soil Research*, *49*(6), 494–503. https://doi.org/10.1071/SR11106

Paritsis, J., Landesmann, J., Kitzberger, T., Tiribelli, F., Sasal, Y., Quintero, C., … Nuñez, M. (2018). Pine plantations and invasion alter fuel structure and potential fire behavior in a patagonian forest-steppe ecotone. *Forests*, *9*(3), 117. https://doi.org/10.3390/f9030117

Parker, I. M., Simberloff, D., Lonsdale, W. M., Goodell, K., Wonham, M., Kareiva, P. M., … Goldwasser, L. (1999). Impact: Toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, *1*(1), 3–19. https://doi.org/10.1023/a:1010034312781

Peltzer, D. A., Bellingham, P. J., Kurokawa, H., Walker, L. R., Wardle, D. A., & Yeates, G. W. (2009). Punching above their weight: Low-biomass non-native plant species alter soil properties during primary succession. *Oikos*, *118*(7), 1001–1014. https://doi.org/10.1111/j.1600-0706.2009.17244.x

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., … Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*(3), 167–234. https://doi.org/10.1071/BT12225

Poorter, L., Lianes, E., Moreno-de las Heras, M., & Zavala, M. A. (2012). Architecture of Iberian canopy tree species in relation to wood density, shade tolerance and climate. *Plant Ecology*, *213*(5), 707–722. https://doi.org/10.1007/s11258-012-0032-6

Pyšek, P., Jarošík, V., Hulme, P. E., Pergl, J., Hejda, M., Schaffner, U., & Vilà, M. (2012). A global assessment of invasive plant impacts on resident species, communities and ecosystems: The interaction of impact measures, invading species' traits and environment. *Global Change Biology*, *18*(5), 1725–1737. https://doi.org/10.1111/j.1365-2486.2011.02636.x

Qi, Y., Jolly, W. M., Dennison, P. E., & Kropp, R. C. (2016). Seasonal relationships between foliar moisture content, heat content and biochemistry of lodgepole line and big sagebrush foliage. *International Journal of Wildland Fire*, *25*(5), 574–578. https://doi.org/10.1071/WF15156

Reich, P. B., Oleksyn, J., & Tjoelker, M. G. (1996). Needle respiration and nitrogen concentration in Scots pine populations from a broad latitudinal range: A common garden test with field-grown trees. *Functional Ecology*, *10*(6), 768–776. https://doi.org/10.2307/2390512

Reinhardt, E., Scott, J., Gray, K., & Keane, R. (2006). Estimating canopy fuel characteristics in five conifer stands in the western United States using tree and stand measurements. *Canadian Journal of Forest Research*, *36*(11), 2803–2814. https://doi.org/10.1139/x06-157

Ricciardi, A., Hoopes, M. F., Marchetti, M. P., & Lockwood, J. L. (2013). Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs*, *83*(3), 263–282. https://doi.org/10.1890/13-0183.1

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, *413*(6856), 591–596. https://doi.org/10.1038/35098000

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., … Essl, F. (2018). Global rise in emerging alien species results from increased accessibility of new source pools. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(10), E2264–E2273. https://doi.org/10.1073/pnas.1719429115

Singh, S. P., Inderjit, Singh, J. S., Majumdar, S., Moyano, J., Nuñez, M. A., & Richardson, D. M. (2018). Insights on the persistence of pines (*Pinus* species) in the Late Cretaceous and their increasing dominance in the Anthropocene. *Ecology and Evolution*, *8*(20), 10345–10359. https://doi.org/10.1002/ece3.4499

Strayer, D. L., Eviner, V. T., Jeschke, J. M., & Pace, M. L. (2006). Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution*, *21*(11), 645–651. https://doi.org/10.1016/j.tree.2006.07.007

Suding, K. N., Lavorel, S., Chapin, F. S. III, Cornelissen, J. H. C., Díaz, S., Garnier, E., … Navas, M.-L. (2008). Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biology*, *14*(5), 1125–1140. https://doi.org/10.1111/j.1365-2486.2008.01557.x

Taylor, K. T., Maxwell, B. D., McWethy, D. B., Pauchard, A., Nuñez, M. A., & Whitlock, C. (2017). *Pinus contorta* invasions increase wildfire fuel loads and may create a positive feedback with fire. *Ecology*, *98*(3), 678–687. https://doi.org/10.1002/ecy.1673

Taylor, K. T., Maxwell, B. D., Pauchard, A., Nuñez, M. A., & Rew, L. J. (2016). Native versus non-native invasions: Similarities and differences in the biodiversity impacts of *Pinus contorta* in introduced and native ranges. *Diversity and Distributions*, *22*(5), 578–588. https://doi.org/10.1111/ddi.12419

Thomaz, S. M., Agostinho, A. A., Gomes, L. C., Silveira, M. J., Rejmánek, M., Aslan, C. E., & Chow, E. (2012). Using space-for-time substitution and time sequence approaches in invasion ecology. *Freshwater Biology*, *57*(11), 2401–2410. https://doi.org/10.1111/fwb.12005

Thomsen, M. S., Olden, J. D., Wernberg, T., Griffin, J. N., & Silliman, B. R. (2011). A broad framework to organize and compare ecological invasion impacts. *Environmental Research*, *111*(7), 899–908. https://doi.org/10.1016/j.envres.2011.05.024

Vilà, M., & Hulme, P. E. (2017). *Impact of biological invasions on ecosystem services*. Basel, Switzerland: Springer.

Wardle, D. A., Bardgett, R. D., Callaway, R. M., & Van der Putten, W. H. (2011). Terrestrial ecosystem responses to species gains and losses. *Science*, *332*(6035), 1273–1277. https://doi.org/10.1126/science.1197479

Wardle, D. A., & Peltzer, D. A. (2017). Impacts of invasive biota in forest ecosystems in an aboveground–belowground context. *Biological Invasions*, *19*(11), 3301–3316. https://doi.org/10.1007/s10530-017-1372-x

Yokomizo, H., Possingham, H. P., Thomas, M. B., & Buckley, Y. M. (2009). Managing the impact of invasive species: The value of knowing the density–impact curve. *Ecological Applications*, *19*(2), 376–386. https://doi.org/10.1890/08-0442.1

Zenni, R. D., Cunha, W. L. D., & Sena, G. (2016). Rapid increase in growth and productivity can aid invasions by a non-native tree. *AoB PLANTS*, *8*. https://doi.org/10.1093/aobpla/plw048

Zenni, R. D., Dickie, I. A., Wingfield, M. J., Hirsch, H., Crous, C. J., Meyerson, L. A., … Le Roux, J. J. (2017). Evolutionary dynamics of tree invasions: Complementing the unified framework for biological invasions. *AoB PLANTS*, *9*(1), plw085. https://doi.org/10.1093/aobpla/plw085

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Sapsford SJ, Brandt AJ, Davis KT, et al. Towards a framework for understanding the context dependence of impacts of non-native tree species. *Funct Ecol*. 2020;34:944–955. https://doi.org/10.1111/1365-2435.13544