



# Variation and genetic parameters of axial resin canal features in clones and families of *Pinus radiata*

James Kudjo Govina<sup>1,2</sup> · Luis A. Apiolaza<sup>2</sup> · Clemens M. Altaner<sup>2</sup> 

Received: 14 May 2019 / Accepted: 10 February 2020  
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## Abstract

Resin canal features are associated with significant economic losses to appearance grade *Pinus radiata* timber. This study investigated the variation in resin canal features in young, 2-year-old, *P. radiata*. Axial resin canal size, density and relative cross-sectional area were determined in twenty families and ten clones from images of microtomed sections, scanned with polarised light to highlight resin canals. Axial resin canal size was generally homogeneous with a mean value estimate of 0.02 mm<sup>2</sup>, and a coefficient of variation of ~10%. Estimated mean values for axial resin canal density and relative area were more variable (coefficients of variation ~30%) and lower for clones (0.69 canals/mm<sup>2</sup> and 1.13%, respectively) than for families (0.90 canals/mm<sup>2</sup> and 1.53%, respectively). Narrow-sense heritability ( $h^2$ ) estimates of the studied axial resin canal features in radiata pine at age 2-years-old were ~0.30. Modulus of elasticity and longitudinal shrinkage were moderately correlated with axial resin canal density and relative area, while basic density and volumetric shrinkage were independent of axial resin canal features. The study indicated that there could be potential for breeding *P. radiata* for resin canal features, with the aim to improve the grade yields of appearance grade products.

**Keywords** Appearance grade · Heritability · Radiata pine · Stiffness · Wood defect

## Introduction

Resin canals in softwoods are a complex network of tubular structures, oriented in both radial and axial directions (Baas et al. 2004; Bannan 1936), providing the trees with a defence mechanism against pests and pathogens (Franceschi et al. 2005; Hodge and Dvorak 2000; Moreira et al. 2015). Resin canals in pines are lined by a layer of resin-secreting epithelial cells, filling this network with resin. Resin will flow from the canal network to seal wounds and suffocate intruding organisms. While resin canals are always formed in pines, they can also be induced by traumatic events (Bannan 1936; Wu and Hu 1997). Studies concerning the resin features associated with the resilience of trees against pathogens

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✉ Clemens M. Altaner  
Clemens.Altaner@canterbury.ac.nz

<sup>1</sup> CSIR-Forestry Research Institute of Ghana, P. O Box UP 63, Kumasi, Ghana

<sup>2</sup> New Zealand School of Forestry, University of Canterbury, Christchurch, New Zealand

generally concluded that elevated levels of resin features facilitated forest health (Ferrenberg et al. 2014; Franceschi et al. 2005; O'Neill et al. 2002; Rosner and Hannrup 2004).

However, resin features in softwoods have been also investigated for technical reasons. First, resin itself can be a desired resource, for example as a source of turpentine (Fett-Neto and Rodrigues-Correa 2012; Mergen et al. 1955; Neis et al. 2019). Second, especially for appearance grade timber, resin 'blemishes' are the major defect, having been reported to account for up to 58% of downgrades from clear wood in radiata pine (Cown et al. 2011). Two resin features might be distinguished in this regard. Resin pockets, typically of traumatic origin and under environmental control (Woollons et al. 2008) dominating timber downgrades, as well as regularly formed resin canals, which render surfaces unappealing as resin canals are surface indentations, visible even after successful coating. The latter is relevant to this study.

In general, stems with higher resin canal frequencies are associated with higher incidences of resin-related defects (Cown et al. 2011; Yang et al. 2007), but the relationships are not always strong (Ananias et al. 2010). Resin-related defects also influence wood processing, for example resin can increase fouling of saws (Bergstedt and Lyck 2007) and dissolve paint finishes on wood products (Dawson et al. 2002). Contrary, resin canals may be advantageous for preservative treatments and timber drying, as they increase the permeability of the material (Flynn 2007; Keey et al. 2012).

Resin canal features have been reported to vary according to genetic (Hannrup et al. 2004; Li et al. 2017; Mergen et al. 1955) and environmental factors (O'Neill et al. 2002; Rosner and Hannrup 2004). While environmental traits, in particular water stress (Rosner and Hannrup 2004; Woollons et al. 2008) but also nutrient levels (Moreira et al. 2015), were identified to have an effect on resin canal features, genetic control was generally found to be most important in spruce (Hannrup et al. 2004; Rosner and Hannrup 2004).

The aim of this study was to determine the variation in resin canals features for clones and families of the New Zealand radiata pine production population at age 2-years-old and to test if the studied variables were under genetic control. Resin canal features were also related to basic density, modulus of elasticity (MoE) and shrinkage of the same samples.

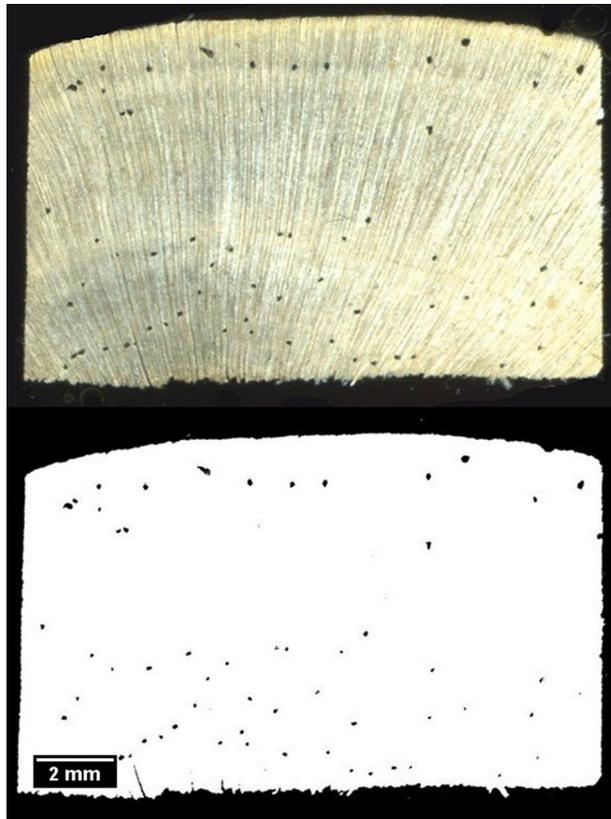
## Materials and methods

### Trial design

Samples were sourced from 2-year-old radiata pine (*Pinus radiata* D. Don) trees planted in a randomized complete block design with 30 replicates at Harewood, Christchurch. Fifty-nine known genotypes (49 full-sibling families and ten clones) of the New Zealand radiata pine breeding population were grown in 75 L bags filled with potting mix containing slow-release fertilizer and drip irrigated (Apiolaza 2014). The family genotypes had been selected for growth and density, whereas clones were selected for growth and stiffness. Three months after planting, the young plants were leaned and tied at a 15° angle for 21 months to separate compression wood from opposite wood (normal wood) (Chauhan et al. 2013).

Twenty out of 49 full-sibling families were selected by using Ranked Set Sampling (Ridout 2003) to collect observations covering the range of both basic density and wood stiffness, while all ten clones were used in this study. For each of the selected families and clones, 10 out of 30 trees were randomly selected and the normal wood samples were used.

**Fig. 1** Scanned wood section in polarized light displaying resin canals as dark dots (top) and after image processing in ImageJ (8-bit, threshold) (bottom)

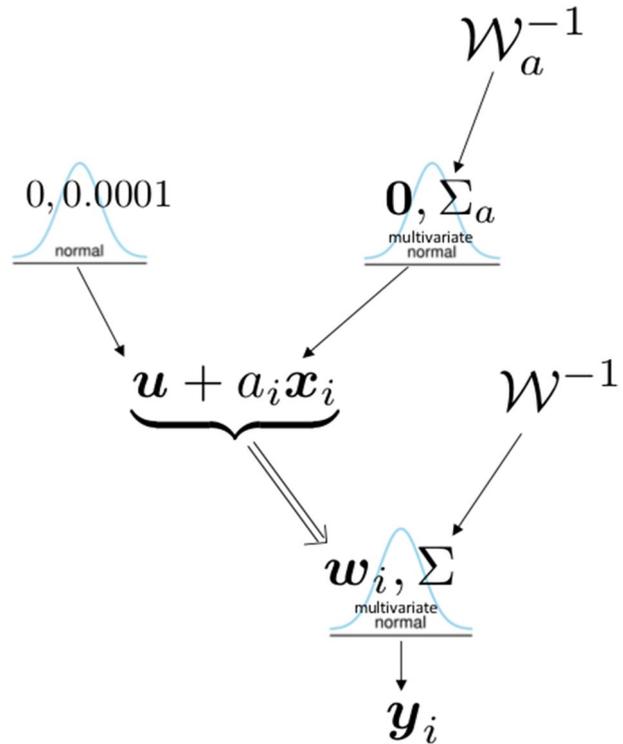


Twenty families and ten clones were included in this study, with 10 replicates each, for a total of 300 trees.

### Measurement of resin canal features

Normal wood samples, ~2 cm in all dimensions and containing the outermost wood were softened at 60 °C for 24 h in distilled water. After cooling the water was replaced with a 1:1 solution of glycerol and ethanol to preserve the wood cubes (Thomas and Collings 2017). Sections ranging from 20 to 60  $\mu\text{m}$  were cut from the cross-sectional surface of the softened wood using a sledge microtome (HM 400, Microm, Walldorf, Germany) and temporarily mounted on a specimen slide in glycerol. One section per tree was scanned with linear polarised light in colour at 2400 dpi resolution using a flatbed scanner (Epson Perfection V700) (Thomas and Collings 2017). Images (Fig. 1) were processed and analysed in ImageJ (Abràmoff et al. 2004). The area ( $\text{mm}^2$ ) of the wood sections, the number of resin canals within the section and the size of each resin canal ( $\text{mm}^2$ ) within the section were extracted automatically from each of the 300 images with ImageJ macros. The data collected were used to calculate the axial resin canal density, defined as resin canal count divided by the area of the section and the relative resin canal area, defined as the average canal size multiplied by the number of canals divided by the area of the section.

**Fig. 2** Directed acyclical graph modified following Kruschke (2010) representing the multivariate hierarchical model for estimating genetic parameters



### Density, modulus of elasticity (MoE), and shrinkage data

All wood samples had been previously assessed for basic density, MoE, longitudinal and volumetric shrinkage following the methods described by Chauhan et al. (2013). Mean basic density, MoE, longitudinal and volumetric shrinkage of opposite wood in the samples were  $295 \text{ kg/m}^3$ ,  $2.63 \text{ GPa}$ ,  $0.79\%$  and  $18.21\%$ , with coefficients of variation of  $6.05\%$ ,  $14.84\%$ ,  $39.03\%$  and  $24.90\%$ , respectively (Apiolaza 2014). The trial showed large variability in wood properties at young age with moderate to high genetic control.

### Statistical analysis

The dataset was analysed using the R statistical software (R Core Team 2016). The genetic analysis adopted a hierarchical-bayesian approach to estimate the posterior distributions for the heritabilities and additive genetic correlations between the assessed traits. The statistical model included an overall intercept and additive genetic effects for each of the traits (Fig. 2). Replicate effects were negligible and eliminated from the model. The vector  $\mathbf{y}_i$  stacks the assessments for each tree sample, so  $\mathbf{y}_i$  follows a multivariate normal distribution ( $\mathbf{w}_i, \Sigma$ ) with expected value  $\mathbf{w}_i$  and a multivariate residual  $\Sigma$ .  $\Sigma$  was given a vague inverse Wishart prior ( $W^{-1}$ ). As the data comprised a mix of clonal and controlled pollination individuals, the analysis uses a multivariate, individual tree (animal) model. The predicted values for the traits of the  $i$ th tree sample was represented as a function of an overall intercept for each trait and the additive genetic effect for each trait ( $a_i x_i$ ). The relatedness

between individuals was accounted for via a numerator relationship matrix derived from the parental relationships between families and clones. Non-additive genetic effects were ignored, as the opportunistic mating design and sample size were inappropriate to properly estimate them.

The model was fitted using Markov Chain Monte Carlo methods implemented in the R software package MCMCglmm (Hadfield 2010). The model was run for 510,000 iterations, with a burn-in period of 10,000. The chain was thinned keeping one every 500 samples for the genetic parameters. Posterior distributions of heritability ( $h^2$ ) and genetic correlations between two traits ( $r_{12}$ ) were estimated using the standard formulas:

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_e^2} \quad \text{and} \quad r_{12} = \frac{\sigma_{a12}}{\sqrt{\sigma_{a1}^2 \sigma_{a2}^2}}$$

where  $\sigma_a^2$  corresponds to the additive genetic variance,  $\sigma_{a12}$  to additive genetic covariance between two traits, and  $\sigma_e^2$  to the residual variance.

## Results and discussion

### Variability in resin canal features

The axial resin canal features considered in this study were size, density and relative cross-sectional resin canal area (Table 1). Axial resin canal size in 2-year-old *P. radiata* was similar for clones (0.0165 mm<sup>2</sup>) and families (0.0170 mm<sup>2</sup>). The estimated mean axial resin canal cross-sectional area of 0.017 mm<sup>2</sup> (Table 1), equating to a diameter of approximately 150 µm, fell into the reported diameter range of 100–200 µm for axial resin canals of this species (Cown et al. 2011). However, the size was smaller than the reported average resin canal size of 0.028–0.036 mm<sup>2</sup> for harvest-sized *P. radiata* trees (Ananias et al. 2010; Yang et al. 2007). The reported increase in axial resin canal size with cambial age in young trees could account for this difference (Ananias et al. 2010; Boschiero Ferreira and Tomazello-Filho 2012; Reid and Watson 1966; Yang et al. 2007). Axial resin canal sizes have also been reported for other pines. For example, reported values were ~0.018 mm<sup>2</sup> for 7-year-old *P. taeda* (Westbrook et al. 2015), 0.024–0.044 mm<sup>2</sup> for 18-year-old *P. elliottii* (Neis et al. 2019), 0.012–0.018 mm<sup>2</sup> (122–150 µm in diameter) for 35-year-old *P. caribaea*

**Table 1** Summary statistic for axial resin canal features in xylem of 2-year-old *P. radiata* clones and families

Variable	Plant type	Mean	95% confidence interval		<i>p</i> value of the difference between means	Coefficient of variation
			Lower	Upper		
Resin canal density (number/mm <sup>2</sup> )	Clone	0.69	0.65	0.73	4.73e–12	31.4
	Family	0.90	0.87	0.94		27.8
% Resin canal area	Clone	1.13	1.06	1.20	1.95e–14	30.7
	Family	1.53	1.47	1.59		28.3
Resin canal size (mm <sup>2</sup> )	Clone	0.0165	0.0161	0.0169	0.0186	11.9
	Family	0.0170	0.0168	0.0173		10.1

var. *hondurensis* (Boschiero Ferreira and Tomazello-Filho 2012), 0.035–0.045 mm<sup>2</sup> for 75-year-old *P. pinaster* (Rodríguez-García et al. 2014) or 0.003–0.020 mm<sup>2</sup> for *P. contorta* (Ferrenberg et al. 2014; Reid and Watson 1966).

The estimated mean axial resin canal density of 0.69 and 0.90 canals/mm<sup>2</sup> (Table 1) agreed with estimates for 14-year-old *P. radiata* of 0.5–1.5 canals/mm<sup>2</sup> (Ananias et al., 2010). While these authors did not observe a radial pattern, a more intensive study of resin canals in *P. radiata* found a clear increase in axial resin canal density with annual ring number (Yang et al. 2007); a result also reported for *P. caribaea* var. *hondurensis* (Boschiero Ferreira and Tomazello-Filho 2012). This radial trend could contribute to the slightly lower axial resin canal density in this dataset, which was based on young 2-year-old trees. Reported values for other pines were ~0.4 canals/mm<sup>2</sup> for *P. taeda* (Westbrook et al. 2015), 0.52 canals/mm<sup>2</sup> for *P. caribaea* var. *hondurensis* (Boschiero Ferreira and Tomazello-Filho 2012), 0.51–0.76 canals/mm<sup>2</sup> for *P. pinaster* (Rodríguez-García et al. 2014), 0.13–0.30 canals/mm<sup>2</sup> for *P. elliottii* (Neis et al. 2019) or ~1 canals/mm<sup>2</sup> for *P. contorta* and *P. flexilis* (Ferrenberg et al. 2014).

The relative area covered by axial resin canals was 1.13% and 1.53% for clones and families, respectively (Table 1). This was comparable to the ~1 to 3% of relative axial resin canal area in *P. pinaster* (Moreira et al. 2015; Rodríguez-García et al. 2014) or the 0.2–0.9% in *Picea abies* xylem (Luostarinen et al. 2017).

Axial resin canal density and percentage area in 2-year-old *P. radiata* xylem had similar variability with coefficients of variation of approximately 30% (Table 1). Similar coefficients of variation were reported for axial resin canal density in equally young *P. radiata* (coefficient of variation 22–29%) (Thomas and Collings 2017) and for 19-year-old *Picea abies* clones (coefficient of variation ~26%) (Hannrup et al. 2004). The size of the axial resin canals were, with a coefficient of variation of approximately 10%, more homogeneous than their occurrence (Table 1). While larger in magnitude, in agreement to this study, the variation in axial resin canal size was found to be three to four times lower than for resin canal density and relative resin canal area in *Picea abies* (Luostarinen et al. 2017).

For all variables, the full-sibling families had higher estimated mean values than the clones (Table 1). These differences were less significant ( $p=0.0186$ ) for canal size. However, for all the variables, more variability was present among clones than families, indicating that the clones were more different from each other than the families. As a consequence larger genetic gain can be achieved by selection from the clones compared to the families.

## Heritability and genetic correlations

The estimated narrow-sense heritabilities ( $h^2$ ) for axial resin canal density ( $h^2=0.33$ ), relative area ( $h^2=0.31$ ) and size ( $h^2=0.31$ ) in 2-year-old *P. radiata* (Table 2) were comparable to estimated heritabilities for other wood properties in similarly aged *P. radiata*, including

**Table 2** Median and 95% credible intervals, in parenthesis, for posterior distributions for heritability (diagonal) and genetic correlations (off diagonal) of axial resin canal features in *P. radiata*

Parameter	Canal size	Canal density	% canal area
Canal size	0.31 (0.25, 0.38)		
Canal density	0.00 (−0.26, 0.24)	0.33 (0.22, 0.46)	
% Canal area	0.00 (−0.27, 0.24)	0.69 (0.51, 0.83)	0.31 (0.18, 0.46)

density and shrinkage (Apiolaza et al. 2011). These narrow-sense heritability values also fell close to the, typically higher, broad-sense heritabilities ( $H^2$ ) for resin canal features in *Picea abies*. Broad-sense heritabilities of  $H^2=0.41$  and  $0.46$  were reported for axial resin canal density at age 19-years-old (Hannrup et al. 2004), while broad-sense heritabilities for radial resin canal density, relative area and size at age 17-years-old were  $H^2=0.21-0.81$ ,  $H^2=0.45-0.66$  and  $H^2=0.46-0.75$ , respectively (Rosner and Hannrup 2004). However, lower  $H^2$  values were reported for resin canal density ( $\sim 0.2$ ) and size ( $< 0.05$ ) in 7-year-old *P. teada* (Westbrook et al. 2015).

Another resin canal related trait, which has been investigated for genetic control in *P. radiata*, was external resin bleeding with a reported narrow-sense heritability of 0.3 (Kumar 2004; Li et al. 2017)

Axial resin canal density correlated strongly and positively ( $r_g=0.69$ ) to the cross-sectional relative axial resin canal area with a narrow (0.51, 0.83) 95% credible interval (Table 2). On the contrary, axial resin canal size was not correlated to the other measured resin canal features. This matched the observation in 17-year-old *Picea abies*, where a strong and consistent genetic correlation was found among clonal trials between radial resin canal density and their relative area, while no consistent genetic correlation was found between radial resin canal size and the other traits (Rosner and Hannrup 2004).

These results suggest that breeding to reduce resin canal density would automatically reduce the relative axial resin canal area. This was not surprising given the homogeneous size of the resin canals. Resin canal size would need to be independently addressed in a breeding programme. However, the low variability of the trait limits the achievable change.

Basic density, MoE, volumetric and longitudinal shrinkage are important physical properties which influence wood utilization. Mean values for the clones and families from the same samples (Apiolaza 2014), were correlated with means of axial resin canals features estimated in this study (Table 3). Axial resin canal size was independent of the other measured wood properties. This was probably attributed to the relatively homogeneous size of the axial resin canals (Table 1). Basic density and volumetric shrinkage were independent of the axial resin canal features for the 2-year-old radiata pine trees, suggesting that breeding to influence resin canal features should not affect basic density or volumetric shrinkage. No direct causality between the resin and basic density would be expected, considering the small volume proportion of axial resin canals of less than 2% (Table 1) combined with a typically low (approximately 1.5% dry weight) resin content in *P. radiata* sapwood (Bamber and Burley 1983; Moore et al. 2014). The results also matched those reported for *Picea abies* (age 19), where no correlation between density and axial resin canal density was found (Hannrup et al. 2004).

Interestingly, axial resin density and relative axial resin canal area were moderately correlated to MoE and longitudinal shrinkage. As the correlations were negative for MoE and positive for longitudinal shrinkage, these axial resin canal features appear to be positively

**Table 3** Correlation coefficients ( $p$  value in parentheses) for resin canals features against selected physical properties of 2-year-old radiata pine wood

Parameter	Canal density	% Canal area	Canal size
Basic density	0.02 (0.74)	0.03 (0.60)	0.05 (0.36)
MoE	-0.29 (<0.001)	-0.32 (<0.001)	-0.09 (0.11)
Volumetric shrinkage	0.07 (0.23)	0.08 (0.15)	0.01 (0.82)
Longitudinal shrinkage	0.21 (<0.001)	0.25 (<0.001)	0.07 (0.26)

correlated to microfibril angle. The underlying physical causality is unclear. Hannrup et al. (2004) did not observe such a relationship between microfibril angle and axial resin canal density in *Picea abies*, probably due to the older age of the investigated trees, which typically have a low and consistent microfibril angle. Considering a breeding programme, a decrease in axial resin canal density and relative area would result in an increase in mean MoE and a decrease in mean longitudinal shrinkage. In both cases, this is a favourable correlation because a high MoE and low longitudinal shrinkage are the desired traits for *P. radiata* (Apiolaza 2014).

It is worth mentioning that the clones were selected for growth and stiffness, whereas the families were bred for growth and density. Hence, the clones would be expected to have lower resin canal features as the families (Table 1).

These observations were conducted with young, 2-year-old, trees on a single site. Resin canal features were reported to be extremely stable across sites (Hannrup et al. 2004; Rosner and Hannrup 2004), suggesting that making use of a single site is sufficient. The fact that resin canal features are known to increase radially (Ananias et al. 2010; Yang et al. 2007) indicates that resin defects become more critical at older age. Consequently, a strong age–age correlation is needed if early assessment is to lead to a superior crop at harvest age (Apiolaza 2009). It would be prudent to confirm the stability of the rankings calculated at 2-years-old from one site at older age for multiple sites. Furthermore, resin related traits have been associated with the ability of the trees to react to pests (Ferrenberg et al. 2014) and therefore unintended effects on tree health when minimising resin canals for wood quality and vice versa should be considered.

## Conclusions

Of the investigated axial resin canal features, density and relative area were highly variable and strongly correlated, while size was more homogenous and not correlated to the other features. As frequency of axial resin canals was variable and heritable in 2-year-old radiata pine (Tables 1, 2), they could be included in a breeding programme. The favourable correlations of resin canal features with wood stiffness and longitudinal shrinkage (Table 3) would make it easier to find superior individuals, which produce high quality appearance-grade timber. This correlation could also explain the overall lower number of resin canal features in the investigated clones compared to the families of the commercial radiata pine breeding population, as the clones had been selected for stiffness.

However, as resin canal features are positively correlated to forest health (Ferrenberg et al. 2014; Franceschi et al. 2005; Westbrook et al. 2015), such radiata pine genotypes selected for lower levels of resin canal features might be more susceptible to pests. Alternatively selecting radiata pine genotypes for higher levels of resin canal features could be an option to improve forest health, with the consequence of reduced appearance quality of the timber.

**Authors' contributions** JKG conducted the experiments, analysed the data and prepared the manuscript draft; LAA assisted with data analysis and revised the manuscript; CMA conceived the study, provided technical advice and revised the manuscript.

**Funding** James Govina received a New Zealand Development Scholarship (NZDS). The trial was funded by the New Zealand Radiata Pine Breeding Company. The trial was managed by John C. F. Walker and Monika Sharma (NZ School of Forestry, NZ).

## Compliance with ethical standards

**Conflict of interest** The authors declare no competing interest.

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