Contrasting xylem vessel constraints on hydraulic conductivity between native and non-native woody understory species

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INTRODUCTION

Wood xylem vessel members constitute the main pathway for water transport over long distances within a plant and are morphologically diverse across species. In addition to the pronounced differences in ring-porous vs. diffuse-porous species, xylem arrangement follows a continuum of organizational levels. Vessel organization and distribution including vessel number and frequency are associated with varying patterns of community assembly and adaptive variation in growth strategies across phylogenetic groups (Baas, 1986). Moreover, correlations between wood anatomical traits (e.g., porosity type, variation in bordered pits and perforation types) and factors integrating seasonal water availability may reveal characteristics representing successful plant hydraulic properties such as water-use efficiency, conductivity, and vulnerability to cavitation (Jansen et al., 2004; Taneda and Sperry, 2008) that promote a physiological advantage of non-native over native species (Pratt and Black, 2006; Caplan and Yeakley, 2010).

High relative growth rate (RGR) is common to many introduced non-native woody plants (Dawson et al., 2011). Hydraulic architecture is associated with plant growth rate (Brodribb et al., 2002; Meinzer et al., 2010), with xylem vessel structure and size identified as the main constraints on maximum water transport and thus hydraulic conductivity (Tyree and Ewers, 1991; Steppe and Lemeur, 2007). Woodrum et al. (2003) examined xylem vessel anatomy and hydraulic conductivity of maples (Acer) of varying growth rates but few differences in hydraulic conductivity or anatomical xylem vessel characteristics were apparent. Pratt and Black (2006) were also unable to find differences in cavitation resistance or xylem specific conductivity between five pairs of co-occurring native and non-native trees. However, few if any studies on the relationship between vessel conduit anatomy and water transport in native vs. non-native species have been performed to date. Yet, trends in species’ hydraulic conductivity have been broadly categorized by means of xylem conduit diameter and rate of water flow (efficiency; Tyree et al., 1994), and that there exists a positive relationship between vessel diameter (VD) and growth rate.

Plant water-use strategies are often evaluated as functional trade-offs that maximize resource capture and retention rates based on the resident environment (Grime, 2001). Non-native species with invasive potential are considered a threat to native plant communities due to more efficient resource-use (Grotkopp et al., 2002; Funk and Vitousek, 2007; Drenovsky et al., 2012) or higher resource use and capture (Cavaleri and Sack, 2010) such that they effectively out-compete natives in their introduced range (Davis et al., 2000; Drenovsky et al., 2012). One way in which non-natives may increase their efficiency is by decreasing the cost of acquiring or using resources. By investing in cheaper structural tissues (Dale and Causton, 1992), species lose benefits associated with increased construction cost which, in turn, influences species’ hydraulic vulnerability to water stress or freezing (Carlquist, 1977). Elucidating the linkage between wood characteristics and water transport provides insight into plant hydraulic functional strategies (Baas, 1986; Taneda and Sperry, 2008).

Emboli sm vulnerability places a constraint on maximum water transport through a reduction in hydraulic conductance as a consequence of drought and freeze-thaw cycles (Pockman and
Sperry, 1996; Meinzer et al., 2001) and even normal growth conditions (Cochard and Tyree, 1990; Sperry et al., 1994; McCully et al., 1998). Recent studies have emphasized additional vessel characteristics that are potentially important drivers of hydraulic transport and protection against embolism formation, including inter-vessel pit structure and size as a bottleneck to air-seeding (Jansen et al., 2004; Choat et al., 2008; Christman et al., 2009; Lens et al., 2011), vessel perforation plate type (openings at the end of vessel elements; Jansen et al., 2004), vessel wall thickness (Hacke et al., 2001), and vessel connectivity (Loepfe et al., 2007; Lens et al., 2011). Comparative studies that investigate vessel characteristics over a wide survey of plant species are limited (but see Jansen et al., 2004; McCulloh et al., 2010).

Here we examine the hydraulic properties of 82 native and non-native woody species common to forests of Eastern North America, including several congeneric groups, which represent a range of anatomical wood types. Broad surveys containing a large number of species have the potential to reveal functional classification syndromes that relate to plant productivity (Zanne et al., 2010). Our goal was to compare relationships between hydraulic conductance and theoretical xylem vessel vulnerability by stem vascular structure and arrangement between non-native and native woody species. We examined relationships between stem xylem vessel anatomical arrangement, xylem vessel types, stem specific hydraulic conductivity, wood development/timing of vessel development, and cavitation vulnerability index among native and non-native woody understory species, as well as differences in water-use efficiency between native and non-native individuals. The use of an index to examine potential stem vulnerability is a useful metric when examining larger data sets that represent several species. Specifically, we tested the hypothesis that non-native understory species have greater capacity for water transport than native understory species.

MATERIALS AND METHODS
PLANT MATERIAL AND GROWING CONDITIONS
Stem material was harvested from mature plants in a common garden comprised of a homogenous, clay loam soil in Syracuse, NY, USA (43°03’N, 76°09’W), representing a range of native and non-native woody species including several common genera (Table 1). At the time of harvest, individuals were approximately the same size and age and maintained under the same condition. Each species was grown in three replicate blocks, each under 80% shade cloth during the growing season (late May—late October) to simulate deciduous forest conditions. Species were under 80% shade cloth during the growing season (late May—late October) to simulate deciduous forest conditions. Species were grown in three replicate blocks, each of the same size and age and maintained under the same conditions (Jansen et al., 2004; Choat et al., 2008; Christman et al., 2009; Lens et al., 2011), vessel perforation plate type (openings at the end of vessel elements; Jansen et al., 2004), vessel wall thickness (Hacke et al., 2001), and vessel connectivity (Loepfe et al., 2007; Lens et al., 2011). Comparative studies that investigate vessel characteristics over a wide survey of plant species are limited (but see Jansen et al., 2004; McCulloh et al., 2010).

Table 1. Here we examine the hydraulic properties of 82 native and non-native woody species common to forests of Eastern North America, including several congeneric groups, which represent a range of anatomical wood types. Broad surveys containing a large number of species have the potential to reveal functional classification syndromes that relate to plant productivity (Zanne et al., 2010). Our goal was to compare relationships between hydraulic conductance and theoretical xylem vessel vulnerability by stem vascular structure and arrangement between non-native and native woody species. We examined relationships between stem xylem vessel anatomical arrangement, xylem vessel types, stem specific hydraulic conductivity, wood development/timing of vessel development, and cavitation vulnerability index among native and non-native woody understory species, as well as differences in water-use efficiency between native and non-native individuals. The use of an index to examine potential stem vulnerability is a useful metric when examining larger data sets that represent several species. Specifically, we tested the hypothesis that non-native understory species have greater capacity for water transport than native understory species.

HYDRAULIC CONDUCTIVITY AND WUE MEASUREMENTS
Three terminal branch stems of similar diameter containing 1 year’s growth were randomly sampled from individuals of each species from each of three replicate blocks in November 2011. Stems were kept moist in damp paper towels in a cooler ~2 h prior to taking measurements in a temperature-controlled room at 25°C, equal to the temperature of the high pressure flow meter (HPFM) (Dynamax Inc., Houston, TX, USA). Diameter and stem length were recorded, and the cortex was shaved from the proximal end of stems prior to attachment to a HPFM.

Stem hydraulic conductance ($K_h$) was measured directly with the HPFM, using methods described by Tyree et al. (1995). Each measurement was recorded ~30 s after stems had a visible flow of water through the end of the stem. Conductance ($K_h$, kg s MPa$^{-1}$), the inverse of resistance, was measured by the force of pressurized water through the stem ($P$) (MPa m$^{-1}$) and the rate of water flow ($F$) (Kg s$^{-1}$). Conductance was calculated as the slope of the regression plot $F$ vs. $P$:

$$K_h = dF/dP$$  \hspace{1cm} (1)

Stem hydraulic measurements were conducted using quasi-steady state, where $F$ and $P$ are approximately constant (Tyree et al., 1993, 1995). Specific stem hydraulic conductivity ($K_s$) was calculated factoring out the variation in stem length and diameter cross-sectional area (kg s MPa$^{-1}$ mm$^{-3}$, Sperry et al., 1988).

Photosynthesis was monitored monthly for each individual at intensities of 800, and 100 mmol photon$^{-2}$ s$^{-1}$, 700 mmol s$^{-1}$flow rate, 20°C (Fridley, 2012). WUE was calculated as the ratio of carbon fixed to water lost, (Li-COR 6400, Inc., Lincoln, NE, USA) (C uptake/transpiration rate, in units of micromol CO2 per mmol H2O).

ANATOMICAL MEASUREMENTS
Two to three stem segments used for hydraulic conductivity were used for anatomical sectioning following conductivity measurements. In addition, three supplemental stem segments collected from the same plants in November 2010 were also sectioned for anatomical measurements. One cm long segments in random locations were removed from the stem, immediately preserved in formalin-acetic acid-alcohol solution (FAA), and stored at room temperature until the embedding process. Samples were dehydrated in a series of ethanol-tertiary butanol (TBA) dilutions before infiltration with pure TBA (Ruzin, 1999).

Stem anatomical samples were embedded in successive changes of Paraplast Plus embedding medium (McCormick Scientific, Saint Louis, Missouri, USA) in a 60°C drying oven for 2 days. Samples were embedded in a final paraffin change hardened with 15% (v:v) paramount (Fischer Scientific, Fair Lawn, New Jersey, USA). Transverse cross-sections were cut at 20 μm increments using a rotary microtome (HM 355S, Microm International GmbH, Walldorf, Germany). Cross sections were stained with saffronin-O [1% (w:v) in 50% ethanol] and counterstained using fast-green [0.1% (w:v) in 1:1 absolute ethanol and clove oil] in a series with histo-clear (National Diagnostics, Atlanta, Georgia, USA) to remove paraffin.

Five images per stem were randomly selected for imaging using 20x magnification with a compound light microscope with a fixed camera attachment (Olympus Imaging Corp., Tokyo, Japan). Images representing 0.77 mm$^2$ cross sectional area were first processed through Photoshop (CS5; Adobe Systems Inc., Mountain View, CA). Images were then cropped and measured using the leucos of the microscope to establish the same cross sectional area for each sample. Images were then analyzed using Image J and results are reported as mm$^{-2}$ of cross sectional area.
Table 1 | Woody shrub species list tested and attributes.

| Species | Family | Invasive status | Porosity type | Perforation plate type | VD (µm) | VF (N/mm²) | VI (VD/VF) | Kₛ (10⁻³ kg s MPa⁻¹ m⁻³) |
|---------|--------|-----------------|---------------|------------------------|---------|------------|------------|-------------------|
| Acer negundo | Sapindaceae | Native | Diffuse | Simple | 21.98 | 42.70 | 0.51 | 3.05 |
| Acer pensylvanicum | Sapindaceae | Native | Diffuse | Simple | 26.40 | 18.80 | 1.40 | * |
| Acer saccharum | Sapindaceae | Native | Diffuse | Simple | 20.35 | 44.90 | 0.45 | * |
| Berberis canadensis | Berberidaceae | Native | Semi-ring | Simple | 12.60 | 80.27 | 0.16 | * |
| Berberis koreana | Berberidaceae | Non-native | Ring | Simple | 16.77 | 62.90 | 0.27 | 8.69 |
| Berberis thunbergii v. atropurpurea | Berberidaceae | Non-native | Semi-ring | Simple | 12.37 | 113.70 | 0.11 | 3.23 |
| Berberis vulgaris | Berberidaceae | Non-native | Ring | Simple | 13.02 | 123.53 | 0.11 | 1.45 |
| Calycanthus floridus | Calycanthaceae | Native | Semi-ring | Simple | 26.00 | 35.70 | 0.73 | * |
| Celastrus orbiculatus | Celastraceae | Non-native | Ring | Simple | 22.11 | 32.10 | 0.69 | 4.52 |
| Celastrus scandens “diana” | Celastraceae | Native | Ring | Simple | 177 | 5767 | 0.31 | 4.97 |
| Cephalanthus occidentalis | Rubiaceae | Native | Ring | Simple | 16.29 | 52.27 | 0.31 | 2.36 |
| Chionanthus virginicus | Oleaceae | Native | Ring | Simple | 20.6 | 24.40 | 0.84 | 3.96 |
| Cornus alternifolia | Cornaceae | Native | Diffuse | Scalariform | 26.43 | 31.20 | 0.85 | 1.12 |
| Cornus amomum | Cornaceae | Native | Diffuse | Scalariform | 28.49 | 30.80 | 0.92 | 3.02 |
| Cornus florida | Cornaceae | Native | Diffuse | Scalariform | 17.80 | 32.50 | 0.55 | * |
| Cornus mas | Cornaceae | Non-native | Diffuse | Scalariform | 15.91 | 28.60 | 0.56 | 5.45 |
| Cornus sericea | Cornaceae | Native | Diffuse | Scalariform | 23.6 | 70.60 | 0.33 | 6.23 |
| Diervilla lonicera | Caprifoliaceae | Native | Diffuse | Scalariform | 25.30 | 55.20 | 0.46 | 0.98 |
| Diervilla rivularis | Caprifoliaceae | Native | Diffuse | Scalariform | 22.60 | 42.40 | 0.53 | * |
| Dirca palustris | Thymelaeaceae | Native | Diffuse | Simple | 15.5 | 68.20 | 0.23 | 0.58 |
| Elaeagnus angustifolia | Elaeagnaceae | Non-native | Diffuse | Simple | 24.40 | 19.10 | 1.28 | * |
| Elaeagnus commutata | Elaeagnaceae | Native | Semi-ring | Simple | 16.50 | 62.36 | 0.26 | * |
| Elaeagnus multiflora | Elaeagnaceae | Native | Ring | Simple | 26.68 | 35.60 | 0.81 | 7.59 |
| Elaeagnus pungens | Elaeagnaceae | Native | Diffuse | Simple | 13.30 | 65.40 | 0.16 | * |
| Elaeagnus umbellata | Elaeagnaceae | Non-native | Semi-ring | Simple | 25.80 | 28.27 | 0.91 | * |
| Euonymus alatus | Celastraceae | Native | Diffuse | Simple | 15.88 | 56.00 | 0.28 | 1.29 |
| Euonymus americanus | Celastraceae | Native | Ring | Simple | 11.70 | 142.00 | 0.08 | * |
| Euonymus atropurpureus | Celastraceae | Native | Diffuse | Simple | 17.25 | 78.67 | 0.22 | 6.29 |
| Euonymus bungeanus | Celastraceae | Non-native | Diffuse | Simple | 18.18 | 72.40 | 0.25 | 10.1 |
| Euonymus europaeus “atropurpureus” | Celastraceae | Non-native | Semi-ring | Simple | 15.70 | 91.47 | 0.17 | * |
| Euonymus hamiltonianus sieboldianus | Celastraceae | Non-native | Diffuse | Simple | 18.88 | 84.80 | 0.22 | 9.08 |
| Euonymus obovatus | Celastraceae | Native | Semi-ring | Simple | 10.60 | 157.58 | 0.07 | * |
| Euonymus phellomanus | Celastraceae | Non-native | Diffuse | Simple | 13.60 | 104.56 | 0.13 | * |
| Frangula alnus | Rhamnaceae | Non-native | Semi-ring | Simple | 20.8 | 31.30 | 0.66 | 0.25 |
| Frangula caroliniana | Rhamnaceae | Native | Semi-ring | Simple | 25.08 | 32.80 | 0.76 | 16.3 |
| Hamamelis virginiana | Hamamelidaceae | Native | Diffuse | Scalariform | 21.21 | 58.00 | 0.37 | 8.68 |
| Hydrangea arborescens | Hydrangeaceae | Native | Semi-ring | Scalariform | 21.55 | 51.10 | 0.42 | 1.22 |

(Continued)
| Species                      | Family            | Invasive status | Porosity type | Perforation plate type | VD (µm) | VF (N/mm²) | VI (VD/VF) | $K_s$ ($10^{-3}$ kg s MPa⁻¹ m⁻³) |
|------------------------------|-------------------|-----------------|---------------|-------------------------|---------|------------|-------------|-------------------------------|
| Hydrangea paniculata “Floribunda” | Hydrangeaceae     | Non-native      | Diffuse       | Scalariform             | 19.60   | 30.20      | 0.65        | *                            |
| Hydrangea quercifolia        | Hydrangeaceae     | Native          | Semi-ring     | Scalariform             | 24.37   | 50.40      | 0.48        | 0.69                         |
| Kolokowtzia amabilis         | Caprifoliaceae    | Non-native      | Ring          | Scalariform             | 16.46   | 38.40      | 0.43        | 13.6                         |
| Lindera benzoin              | Lauraceae         | Native          | Diffuse       | Simple                  | 16.21   | 36.90      | 0.44        | 0.24                         |
| Lonicera canadensis          | Caprifoliaceae    | Native          | Diffuse       | Simple                  | 13.20   | 83.53      | 0.16        | *                            |
| Lonicera fragrantissima      | Caprifoliaceae    | Non-native      | Semi-ring     | Simple                  | 13.81   | 59.95      | 0.23        | 0.66                         |
| Lonicera hirsuta             | Caprifoliaceae    | Native          | Diffuse       | Simple                  | 17.80   | 87.60      | 0.20        | *                            |
| Lonicera involucrata var involucrata | Caprifoliaceae | Non-native      | Diffuse       | Simple                  | 15.12   | 93.53      | 0.16        | 1.70                         |
| Lonicera japonica “halliana” | Caprifoliaceae    | Non-native      | Diffuse       | Simple                  | 24.70   | 2760       | 0.89        | *                            |
| Lonicera morrowii            | Caprifoliaceae    | Non-native      | Semi-ring     | Simple                  | 15.04   | 51.80      | 0.29        | 0.63                         |
| Lonicera nitida              | Caprifoliaceae    | Non-native      | Semi-ring     | Simple                  | 11.77   | 120.40     | 0.1         | 8.79                         |
| Lonicera oblongifolia        | Caprifoliaceae    | Native          | Semi-ring     | Simple                  | 14.10   | 56.90      | 0.25        | *                            |
| Lonicera periclymenum “GS Thomas” | Caprifoliaceae     | Non-native      | Diffuse       | Simple                  | 24.80   | 44.07      | 0.56        | *                            |
| Lonicera pileata             | Caprifoliaceae    | Non-native      | Semi-ring     | Simple                  | 12.30   | 116.00     | 0.11        | *                            |
| Lonicera ruprechtiana        | Caprifoliaceae    | Non-native      | Semi-ring     | Simple                  | 16.06   | 50.50      | 0.32        | 4.21                         |
| Lonicera sempervirens        | Caprifoliaceae    | Native          | Semi-ring     | Simple                  | 24.92   | 36.00      | 0.69        | 2.47                         |
| Lonicera standishii          | Caprifoliaceae    | Non-native      | Diffuse       | Simple                  | 12.30   | 80.57      | 0.15        | *                            |
| Lonicera tatarica            | Caprifoliaceae    | Non-native      | Semi-ring     | Simple                  | 15.57   | 74.87      | 0.21        | 3.52                         |
| Lonicera villosa var villosa | Caprifoliaceae    | Native          | Semi-ring     | Simple                  | 14.10   | 5750       | 0.25        | *                            |
| Lonicera x bella             | Caprifoliaceae    | Non-native      | Diffuse       | Simple                  | 16.50   | 64.00      | 0.26        | *                            |
| Lonicera xylosteum           | Caprifoliaceae    | Non-native      | Semi-ring     | Simple                  | 15.46   | 69.95      | 0.22        | 1.40                         |
| Ptelea trifoliate            | Rutaceae          | Native          | Ring          | Simple                  | 23.99   | 12.44      | 1.93        | 0.21                         |
| Rhamnus alnifolia            | Rhamnaceae        | Native          | Ring          | Simple                  | 18.90   | 37.80      | 0.50        | *                            |
| Rhamnus cathartica           | Rhamnaceae        | Non-native      | Semi-ring     | Simple                  | 14.40   | 58.80      | 0.24        | *                            |
| Rhamnus davurica             | Rhamnaceae        | Non-native      | Ring          | Simple                  | 14.23   | 84.20      | 0.17        | 11.6                         |
| Ribes rubrum “cherry”        | Grossulariaceae   | Non-native      | Diffuse       | Scalariform             | 16.2    | 60.00      | 0.27        | 1.56                         |
| Rosa multiflora              | Rosaceae          | Non-native      | Diffuse       | Simple                  | 16.09   | 54.17      | 0.3         | 4.65                         |
| Rosa palustris               | Rosaceae          | Native          | Semi-ring     | Simple                  | 19.90   | 48.20      | 0.41        | *                            |
| Sambucus nigra ssp canadensis | Adoxaceae        | Native          | Diffuse       | Simple                  | 2752    | 28.60      | 0.96        | 0.17                         |
| Sambucus racemosa            | Adoxaceae         | Native          | Ring          | Simple                  | 26.45   | 42.00      | 0.63        | 3.46                         |
| Shepherdia argentea          | Elaeagnaceae      | Native          | Ring          | Simple                  | 18.55   | 43.00      | 0.43        | 4.39                         |
| Shepherdia canadensis        | Elaeagnaceae      | Native          | Diffuse       | Simple                  | 16.49   | 85.50      | 0.19        | 2.27                         |
| Stephanandra incisa “crispa” | Rosaceae          | Non-native      | Diffuse       | Simple                  | 16.50   | 34.40      | 0.48        | *                            |
| Viburnum acerifolium         | Adoxaceae         | Native          | Diffuse       | Scalariform             | 14.50   | 68.80      | 0.21        | *                            |
| Viburnum dentatum            | Adoxaceae         | Native          | Diffuse       | Scalariform             | 22.4    | 38.80      | 0.58        | 4.45                         |
| Viburnum dilatatum           | Adoxaceae         | Non-native      | Diffuse       | Scalariform             | 20.06   | 51.53      | 0.39        | 2.32                         |
| Viburnum edule               | Adoxaceae         | Native          | Diffuse       | Scalariform             | 27.22   | 50.20      | 0.54        | 3.93                         |
| Viburnum lantana             | Adoxaceae         | Non-native      | Diffuse       | Scalariform             | 20.54   | 58.10      | 0.35        | 1.16                         |

(Continued)
View, CA, USA) to select and fill each individual vessel, and then analyzed for xylem vessel lumen cross sectional area (VA) using the image-analysis software Image J (National Institute of Health, Bethesda, MD, USA, http://rsb.info.nih.gov/ij/index.html). Vessel area was converted to diameter (VD) assuming circularity of vessels. Conduit-containing sections of each image were then randomly cropped to 0.09 mm² to represent the xylem area of the smallest stem to obtain vessel frequency (VF) over a uniform area for all species. The use of an index can be a valuable metric to examine larger data sets that are compiled across periods of annual wood formation (the first, middle and last row of selected vessels). A linear mixed model was used to test for significant predictors of vessel grouping in secondary xylem, comparing vessel classification we then calculated grouped vessel percentage (the percentage of the number of vessels grouped relative to the total number of vessels), vessel grouping index (mean number of vessels per vessel grouping), and the percentage of solitary vessels relative to the total number of vessels.

### STATISTICAL METHODS

Differences in the distribution of vessel class frequency were assessed between native and non-native understory species using the Chi-square test. Differences in factors predicting conductivity, vessel traits and vulnerability index were tested using mixed-effect models to control for variability from genus classification. A bivariate regression analysis tested for significance in relationships between conductivity and vessel traits, where conductivity and vulnerability index were log-transformed to improve the assumption of normality. A linear 90th quantile regression was performed using the “quantreg” package from R (v. 2.13.1) to estimate the slope of the “packing limit” of vessels, representing the upper limit of the number of vessels that can fit in a given area based on size. Forty-nine of the 82 species, those with conductivity measurements, were analyzed for significance in VD over three distinct rows of xylem vessels, representing three different periods of annual wood formation (the first, middle and last row of selected vessels). A linear mixed model was constructed to determine how time influences vessel sizes between porosity type, origin, and perforation plate type. Genus was included as a random variable, and vessel row was used as an interaction term for time across effects. Vessel grouping in metaxylem was only compared between non-native and native species that had metaxylem using the Mann-Whitney U-test. Each classification of vessel grouping in secondary xylem was compared, respectively between non-native and native species using One-Way analysis of variance (ANOVA). Data were tested for normality and homogeneity to determine if it matched the assumptions of ANOVA. A mixed effects model was used to test for significant predictors of water use efficiency (WUE), using origin and differing light levels across 38 of the 82 species. Species was used as random factor, due to non-independence of repeated measures. Tukey’s HSD post-hoc analysis was performed to distinguish differences between light levels. The relationships between vulnerability index and vessel groupings traits were examined individually by linear regression. All analyses excluding quantile regression were performed using JMP (SAS Institute Inc., Cary, NC, v. 10.0).

### Table 1 | Continued

| Species          | Family          | Invasive status | Porosity type   | Perforation plate type | VD (μm) | VF (N/mm²) | VI (VD/VF) | Kₚ (10⁻³ kg s MPa⁻¹ m⁻²) |
|------------------|-----------------|-----------------|-----------------|------------------------|---------|------------|------------|--------------------------|
| *Viburnum lentago* | Adoxaceae       | Native          | Diffuse         | Scalariform            | 20.30   | 65.00      | 0.23       | 2.40                     |
| *Viburnum nudum* ssp cassanoides | Adoxaceae       | Native          | Semi-ring       | Scalariform            | 17.90   | 62.50      | 0.22       | *                        |
| *Viburnum opulus* | Adoxaceae       | Native          | Diffuse         | Scalariform            | 20.30   | 65.00      | 0.23       | 2.40                     |
| *Viburnum opulus var Americana* | Adoxaceae       | Native          | Diffuse         | Scalariform            | 19.26   | 71.50      | 0.27       | 4.21                     |
| *Viburnum prunifolium* | Adoxaceae       | Native          | Diffuse         | Scalariform            | 15.00   | 46.70      | 0.32       | *                        |
| *Viburnum rafanesquianum* | Adoxaceae       | Native          | Diffuse         | Scalariform            | 16.76   | 66.60      | 0.25       | 26.3                     |
| *Viburnum setigerum* | Adoxaceae       | Non-native      | Diffuse         | Scalariform            | 20.20   | 45.60      | 0.44       | *                        |

Mean vessel traits, VD, vessel diameter; VF, vessel frequency; VI, vulnerability index; and Kₚ, stem hydraulic conductivity, for each species.

*Denotes species without high pressure flow meter (HPFM) data.
RESULTS
Of the 82 species studied, porosity type did not differ with origin \( (P = 0.970) \). When species were separated by porosity type, 55.3% of native species had a diffuse porous xylem ring structure, 29.8% had a semi-ring, and 14.9% had a ring porous vessel. Non-native species had a distribution comprised of 52.6% diffuse porous, 31.6% semi-ring porous, and 15.8% ring porous. However, contributions of some overrepresented genera drove much of the porosity type distribution. When accounting for genus, members of *Viburnum* and *Lonicera* comprised \( \sim 37\% \) of the total individuals, with most species within a genus sharing similar perforation plate type and porosity type traits (Table 1).

VESEL SIZE DISTRIBUTION
The distribution of vessel class frequency differed between native and non-native species \( (P < 0.0001, \text{Figure } 1) \). Vessels with diameters less than 20 \( \mu \text{m} \) appeared more frequently in non-native species than native species. The diameter of more than 50% of the vessels in non-native species ranged from 10 to 20 \( \mu \text{m}, \) in which 33.9% of the vessels had diameters between 10 and 15 \( \mu \text{m}. \) Frequency of the vessels with diameters more than 20 \( \mu \text{m} \) was higher in native species than non-native species. The diameter of more than 70% of the vessels in native species ranged uniformly from 10 to 25 \( \mu \text{m}, \) with the 15–20 \( \mu \text{m} \) interval class having the highest VF, 26.1%.

HYDRAULIC CONDUCTIVITY \( (K_s) \)
The mixed-effects model did not show any effects from porosity, perforation plate or status as native or non-native on hydraulic conductivity \( (P > 0.10) \).

VESEL TRAITS AND VULNERABILITY INDEX
No differences in VD, VF, or VI were found across porosity type, origin or perforation plate type \( (P > 0.10, \text{Table } 3) \). Despite an insignificant difference, non-native species had lower log VI \( (-0.978 \pm 0.167) \) compared with native species \( (-0.880 \pm 0.141) \), which was the result of a lower but significant VD of non-native species at \( \alpha = 0.10 (P = 0.0694) \). Overall, non-native species had smaller vessels and an overall lower vulnerability index.

RELATIONSHIPS BETWEEN VD, VF, VI, VESSEL AREA AND \( K_s \)
A positive relationship was observed between log-transformed vessel area and log-transformed hydraulic conductivity \( (P = 0.033, \text{Figure } 2) \). This indicates faster water movement in species with a higher number of vessels per xylem area than those with less vessel area per unit xylem area (Figure 3). There was no correlation between \( K_s \) and VI \( (P = 0.6677, \text{Figure } 3) \). When VI was divided into the individual components of VD and VF to test for a relationship with \( K_s \), no relationship was found for either VD \( (P = 0.3565) \) or VF \( (P = 0.380) \).

VESEL PACKING
Overall, an inverse relationship between VD and VF was found for both native and non-native species (Figure 4), indicating the larger the conduit diameter, the fewer number of conduits that can occupy a given area of wood. The slope of the constraint line for native species \( (-6.382) \) was steeper than the slope for non-native species \( (-4.909) \).

TIMING OF FORMATION AND INFLUENCE ON VESSEL SIZE
Genera explained 39% of the total variability within the model \( (P < 0.10) \), suggesting that variation among genera contributes to differences in VD. Timing of vessel development was a significant factor \( (P < 0.001) \). In a comparison of vessel rows, the last row of vessels was significantly smaller than that of both the first and middle rows \( (P < 0.10, \text{Table } 2) \). No interaction was detected between timing of vessel development and porosity, perforation plate type, or origin \( (P > 0.10) \). Only origin had an effect on VD \( (P < 0.001) \). Porosity type and perforation plate type had no predictive effect on VD (Table 3). The variability contributed by
FIGURE 3 | Bivariate fit of vulnerability index (VI) vs. the log values of stem conductivity ($K_s$). (A–C) show VI by porosity, (A) by origin (B), and by perforation plate type (C). All relationships with log($K_s$) were not significantly correlated ($P > 0.10$).

vessel row was 16%, compared with 32% for genera. Again, origin was the only significant factor in predicting VD ($P < 0.0001$).

VEssel GROUPINGS
Approximately 62% of non-native species had metaxylem, while only 16% of native species had metaxylem. Comparing the vessel groupings in metaxylem of the non-native species to the few native species that had metaxylem, non-natives had a higher number of vessel groupings in the $\geq$5-vessel grouping class ($P = 0.0184$, Table 3).

In the secondary xylem, native species had significantly more vessel groupings in the 3- ($P = 0.0114$) and 4-vessel grouping classes ($P < 0.0001$). The proportion of vessel groupings to total vessels was also significantly higher in native species, compared with non-natives, in these two categories ($P = 0.0099$ for the 3-vessel grouping class and $P < 0.0001$ for the 4-vessel grouping class). Thus, the vessel grouping index in native species was higher than that in non-native species ($P = 0.0271$); in other words, non-native species had a higher proportion of solitary vessels in the secondary xylem than native species ($P = 0.0277$).

There was a negative linear relationship between average VD and proportion of solitary vessels to total xylem vessels (Figure 5).
suggestion that species with smaller vessels tend to have fewer vessel groupings.

There was a decrease in the vulnerability index with increasing percentage of solitary vessels (Figure 6). Specifically, the vulnerability index decreased with decreasing percentage of vessel groupings in the 2, 3, and 4-vessel grouping classes, but not in ≥5-vessel grouping class (Figure 7).

WATER USE EFFICIENCY
Species represented 68.1% of the total variability in the model relative to the fixed factors, significantly contributing to differences in WUE ($P < 0.0001$). Light level was the only significant predictor of WUE, increasing 0.3 units per increase in light level (Table 4, $P < 0.0001$). Origin had no effect on WUE. All four light levels were significantly different from each other; WUE increased as light levels increased ($P < 0.10$).

DISCUSSION
Hydraulic contrasts in vessels between native and non-native species have been proposed in a number of recent studies (Pratt and Black, 2006; Caplan and Yeakley, 2010; Cavalieri and Sack, 2010). However, we present results from the first study to examine the direct relationship between xylem vessel anatomical characteristics and water flow across such a large diversity of native and non-native woody shrub species. Contrary to our hypothesis, we found non-native woody species possessed smaller secondary xylem vessels compared with native species although the two groups had similar hydraulic conductance (Figures 1, 3). Non-native, fast-growing species are often considered hydraulically efficient in that they exhibit xylem vessel characteristics that confer high water transport and reduced cavitation resistance (Gilbert et al., 2006; Marksteijn et al., 2011). The Hagen-Poiseuille law, which predicts that the hydraulic efficiency of a vessel increases with the fourth power of its diameter (Tyree and Zimmermann, 2002), would suggest that fast-growing non-native species should have wider VD conduits, which would be advantageous for a rapid growth strategy.

No significant differences in WUE efficiency were found between native and non-native species (Table 4, $P = 0.3973$). WUE has been postulated to be an important factor contributing to success of non-natives (Funk and Vitousek, 2007), yet differences in WUE between non-native and native species is contingent upon growth form and climate (Cavalieri and Sack, 2010). In co-occurring species of the same growth form, there is evidence to suggest that native and non-native species do not differ

Table 3 | Vessel grouping in metaxylem and secondary xylem of native and non-native species.

| VESSEL GROUPINGS IN METAXYLEM | Native | Non-native | $P$-value |
|-------------------------------|--------|------------|-----------|
| Number of 2-vessel groupings  | 4.51 (0.00) | 4.84 (0.73) | n.s.      |
| Number of 3-vessel groupings  | 3.10 (0.04) | 3.06 (0.42) | n.s.      |
| Number of 4-vessel groupings  | 1.71 (0.01) | 2.16 (0.29) | n.s.      |
| Number of ≥5-vessel groupings | 1.96 (0.08) | 4.27 (0.82) | 0.0184    |
| 2-vessel grouping (%)         | 21.27 (2.94) | 19.02 (2.94) | n.s.      |
| 3-vessel grouping (%)         | 16.92 (1.36) | 12.08 (1.94) | n.s.      |
| 4-vessel grouping (%)         | 9.83 (1.28) | 7.23 (0.73) | n.s.      |
| >5-vessel grouping (%)        | 9.69 (2.12) | 12.08 (1.22) | n.s.      |
| Vessel grouping index         | 3.14 (0.13) | 3.44 (0.14) | n.s.      |
| Solitary vessels (%)          | 13.97 (4.11) | 22.80 (3.86) | n.s.      |

Table 4 | The effect of porosity type, native status, perforation plate type, and light level on water use efficiency (WUE).

| Factor | WUE | SE  | $F$   | $P$     |
|--------|-----|-----|-------|---------|
| NATIVE STATUS |     |     |       |         |
| Native  | 2.75 | 0.12 | 0.3973 | 0.3973  |
| Non-native | 2.89 | 0.11 |         |         |
| LIGHT LEVEL (PAR $\mu$mol m$^{-2}$ s$^{-1}$) | | | | |
| 50   | 1.38$^a$ | 0.095 | 523.5904 | <0.0001 |
| 100  | 2.27$^b$ | 0.095 |         |         |
| 300  | 3.58$^c$ | 0.095 |         |         |
| 800  | 4.06$^d$ | 0.095 |         |         |

Significant factors are in bold. Different letters in a column indicate significant differences in WUE between light levels at the $P < 0.05$ level.
in WUE, since WUE may act in conjunction with variations in other plant traits to weaken or remove competitive advantages (Daehler, 2003; Funk and Vitousek, 2007; McAlpine et al., 2008; Cavaleri and Sack, 2010).

We found a significant positive correlation between xylem area as a percentage of wood area and hydraulic conductivity, which is consistent with Gleason et al. (2012) who found a positive correlation between xylem area and stem hydraulic conductivity across 120 Australian woody dicot species. However, there was not a relationship between conductivity and conduit traits of diameter and frequency, potential vulnerability index, and categorial porosity type (Figure 2). Since potential vulnerability index was calculated directly from VD, it is unlikely that this measure would relate to $K_s$ given the lack of relationship with VD. There was also no difference in conductivity between simple and scalariform plate types ($P > 0.10$), despite evidence from Christman and Sperry (2010) showing a considerable influence of vessel perforation plate type on xylem flow resistance in scalariform species. This finding may be due to the significant relatedness between individuals, since perforation plate type is conserved within groups of closely related species (Table 1). The relationship between hydraulic conductivity and resistance to cavitation events is well studied, with numerous findings of a trade-off between safety and efficiency (Pockman and Sperry, 2000; Hacke et al., 2006; Sperry et al., 2008; Markesteijn et al., 2011). The extent of this relationship is highly dependent upon adaptation of the xylem vessels (Markesteijn et al., 2011). A lack of difference in hydraulic conductance and potential vulnerability index in our study suggests that non-native plants do not exhibit a hydraulic advantage over native plants, a similar finding to that of Pratt and Black (2006). However, our lack of difference in hydraulic conductance and potential vulnerability index may be attributed to other anatomical factors such as perforation pits, which may account for $>50\%$ of total flow resistance of vessel networks depending on number, size, and structure (Wheeler et al., 2005; Choat et al., 2008; Lens et al., 2011) and conduit
length which is correlated with porosity type and conductivity per xylem cross-sectional area ($K_{XA}$; Zimmermann and Jeje, 1981; Lens et al., 2011). Additionally, our lack of difference may be due to the phyllogenetic relationships among the species tested. Recent findings from Marksteijn et al. (2011) indicate that species differences can account for 62–98% of the variation in vessel traits. In our study, phyllogenetic relatedness accounted for 39–68% of the total variation among traits. Comparing phyllogenetic relatedness of native and non-native plants provided more meaningful explanation of invasive traits (McDowell, 2002; Dawson et al., 2011).

However, phyllogenetic relatedness may constrain morphological and physiological variations between species (Goldberg, 1987), which may explain the lack of difference in vessel traits observed in our study.

Non-native species had much higher ($\geq$ 5) vessel groupings in metaxylem than native species. Metaxylem most likely becomes non-functioning after secondary xylem has developed, but it serves an important function during initial growth as in our species with only 1 year of growth. It is likely that the formation of metaxylem and vessel connectivity play an important role in the high growth rate of many non-native species. Maximum hydraulic conductivity has been found to increase with vessel connectivity (Loepfe et al., 2007). Meanwhile, higher vessel groupings may also increase the vulnerability to cavitation by increasing the probability for the spread of embolism (Loepfe et al., 2007). In contrast to Loepfe et al. (2007), Carlquist (2009), and Lens et al. (2011) stated that vessel grouping would decrease the vulnerability to cavitation since it serves to bypass frequent embolisms by providing alternative routes for water flow. In our study, higher vessel groupings, especially the 2-, 3-, and 4- vessel groupings, showed increasing vulnerability to embolism, supporting the Loepfe et al. (2007) model for the potential of vessel connectivity to promote embolism. Interestingly, non-native species also had a higher proportion of small solitary vessels within their secondary xylem, which could partially explain the lack of difference in $K_v$ between native and non-native species.

Average xylem vessel size was significantly smaller in non-native woody shrub species than in native species. In northern temperate deciduous forests, resistance to cavitation is an important feature in freeze tolerance. Davis et al. (1999) suggested a strong correlation between VD and cavitation by freezing, where small-vessel conduits are relatively resistant to cavitation. Thus, the smaller VD in non-native species may increase the competitive advantage of non-native species by allowing a longer growing season through higher resistance to cavitation from late-season freeze events. In fact, recent work by Fridley (2012) has shown that non-native deciduous plants retain leaves longer through the autumn season than related native species thus allowing prolonged growth.

While our study incorporates abroad range of species, our scope is limited to stem hydraulic conductance, which expressed inversely as resistance might account for a fraction of the total hydraulic resistance of a plant from roots to leaves (Tyree and Ewers, 1991; Becker et al., 1999). Root mean VDs were on average 30% larger than twig vessels in a recent study of tropical trees by Schulte et al. (2013), indicating an 85% increase in theoretical hydraulic conductance, as calculated by the Hagen-Poiseuille law. In future work, having a complete hydraulic architecture of non-native plants may better elucidate competitive mechanisms for water transport in non-native species. Moreover, a thorough evaluation of hydraulic conductance throughout an entire growing season is warranted as we suspect that larger differences in $K_v$ may occur earlier in the spring when non-native species have functional metaxylem during shoot elongation.

**AUTHOR CONTRIBUTIONS**

Taryn L. Bauerle and Jason D. Fridley designed the experiment. Maria S. Smith carried out the measurements. Maria S. Smith and Jingjing Yin performed the data analysis. Maria S. Smith, Taryn L. Bauerle, Jingjing Yin, and Jason D. Fridley prepared the manuscript.

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