

Hybridisation between related taxa has a range of possible biological consequences, ranging from the production of sterile offspring, through introgression of alleles into populations, to the formation of new species. Examples of plant and animal species hybridising with related taxa abound in the New Zealand region. We review New Zealand hybridisation has been demonstrated with cytogenetic and DNA sequence evidence. Hybridisation is highlighted.

"*Equus caballus* × *Equus asinus* hybridisation in New Zealand." *Journal of the Royal Society of New Zealand* 39:15–34.

Hybridisation is the mating and production of offspring between individuals from genetically distinct populations (Harrison 1993). Hybridisation has been variously viewed as either an evolutionary dead-end, or an important evolutionary process, both in the formation of novel species. Hybridisation can create new species (Kraus & Miyamoto 1990;

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<sup>3</sup>Owung *Equus caballus* × *Equus asinus* hybridisation in New Zealand. *Journal of the Royal Society of New Zealand* 39:15–34.

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<sup>5</sup>Dikdik *Equus caballus* × *Equus asinus* hybridisation in New Zealand. *Journal of the Royal Society of New Zealand* 39:15–34.

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Arnold et al. 1991; DeMarais et al. 1992; Bullini 1994; Rieseberg et al. 1995; Coyne & Orr 2004; Schwarz et al. 2005), reinforce barriers between gene pools (Howard 1993; Coyne & Orr 3; ; 9.4226="Ugtxgfkq" ("Pqq4225+. "nk o kv"urgekcvkqp"cpf"cfrcvckqp"\*Ucvmkp"3; ; 9+. "uyc o r" endangered species (Rhymer & Simberloff 1996) or form a bridge for transfer of adaptations among lineages (Arnold 2004).

" Ykvj"vjg"cfxgpp"qh"pgy"igpvyke"vqqnu."Pgy"\gcncpf"dknqiku"jcxg"vcmgp"vjg"qrrqtvwpkv{" to investigate old hypotheses and erect new ones concerning hybridisation. Multilocus monogenic detection of lineages that have arisen via hybridisation. New Zealand has a long history of hybridisation studies in plants especially but there are now many animal examples and even evidence of virus recombination on our shores. In addition, New Zealand has the advantage of arrival of exotic species has been well documented and geological studies give us some ability to date the fragmentation, expansion and hybridisation of our native species. New Zealand mathematicians who are developing novel methods to study hybridisation will continue to give us new insights into the evolution of our native species. New Zealand studies offer new information or a different perspective.

Hybridisation has been at the centre of three debates in evolutionary biology: species concepts, the role of hybridisation in speciation, and the role of hybridisation in the evolution of new species. New Zealand studies offer new information or a different perspective.

Vjg"kf gpkv"Leckvqp"cpf"fgLpkykqp"qh"urgekcu"qhvgp"tghgtu"vq"vjg"cdknkv{" "qh"kpfxkfwcnu"htq o" "fkhhgtgpv"rqrwncvku"vq"o cvg"cpf"rtqfweg"cv"hgucv"uq o g"hgvtkng"qhhu rtkpi"Vjg"dknq i kecn"urgekcu" concept (Mayr 1942) is based on the principle that different species do not exchange genes,

J { dtkfkucvqp"ku" c" eq o o qp"cpf"ko rqtvcvp"gxqnvkqpct{" rtqegu" yqtnfykfgl"Vjg"nqpi/vgt o" qwveq o g"qh"j { dtkfkucvqp"ku"fg r g p f g p v"qp"vjg"tgncvkg"Lyvguu"qh"vjg"j { dtkfu"cpf"uudugswgpp"igp g t c v k p u." compared to the parental taxa, as illustrated by the following New Zealand examples.

<sup>1</sup>*Hemideina ricta* and *H. femorata* \*Oqti cp/Tkejctfu" ("Vqy pugpf"3; ; 7+<sup>2</sup>*Galaxias depressiceps* and *G. anomalus* (Allibone et al. 1996); <sup>3</sup>*Kunzea sinclairii* and *Leptospermum scoparium* (Harris et al. 1992); <sup>4</sup>*Asplenium x lucrosus* (Perrie et al. 2005); <sup>5</sup>*Hemideina thoracica* (Morgan-Richards et al. 2000; Morgan-Richards & Wallis 2003); <sup>6</sup>*Hemideina maori* (King et al. 1996, 2003); <sup>7</sup>*Galaxias depressiceps* and *G. sp D* (Esa et al. 2000); <sup>8</sup>*Kikihia* species (Marshall et al. 2008); <sup>9</sup>*Pseudopanax lessonii* and *P. crassifolius* (Shepherd & Perrie unpubl. data); <sup>10</sup>*Phormium tenax* and *P. cookianum* (Smissen & Heenan 2007; Smissen et al. 2008); <sup>11</sup>*Carpophyllum angustifolium* and *C. maschalocarpum* (Zuccarello et al. unpubl.); <sup>12</sup>*Helichrysum lanceolatum* × *A. bellidioides* (Smissen et al. 2007); <sup>13</sup>*Nothofagus fusca*, *N. truncata*, *N. solandri* var. *cliffortioides* \*Vjq o ugp"4224="Mpcrr"4229+<sup>14</sup>*Himantopus novaezelandiae* and *H. leucocephalus* (Greene 1999; MacAvoy & Chambers 1999; Wallis 1999); <sup>15</sup>*Metrosideros* spp. (Gardner et al. 2004); <sup>16</sup>*Raoulia* spp. \*U o kuugp"gv"cnl"4225="Hqtf"wp r w d n l"fcvc+<sup>17</sup>*Hoheria glabrata* and *H. lyallii* (Heenan et al. 2005); <sup>18</sup>*Coprosma* spp. (Wichman et al. 2002); <sup>19</sup>*Grahamina capito* and *Fosterygion varium* (Hannan 2005); <sup>20</sup>*Brachaspis nivalis* and *B. collinus*\*Vtgykem"4223+<sup>21</sup>*Anas chlorotis*, *A. superciliosa* and *A. platyrhynchos* (Kennedy & Spencer 2000; Barton 2003); <sup>22</sup>*Cyanoramphus forbesi* and *C. novaezelandiae chathamensis* (Chan et al. 2006); <sup>23</sup>*Acanthoxyla* \*Oqti cp/Tkejctfu" ("Vtgykem" 4227="Dwemng {"gv"cnl"422 : +0<sup>24</sup>*Pratia angulata* and *P. perpusilla* (Murray et al. 2004); <sup>25</sup>*Anaphalioides hookeri* (inferred parentage *A. bellidioides* and *A. triner* (Murray )-4C200n241j 05(Pratia )-4Six); ((eciT0 1; (of 1 Tf 11.61

uq"kf gpvkŁecvkqp"qh"j { dtkfu"jcu"dgpp"qh"hw pfc o gpvcn"ko rqtvcpeg"kp"vjg"tguqnwvkqp"qh"urgekguø boundaries. Sometimes distinct populations that are involved in hybridisation are regarded cu"o g o dgtu"qh"fkhhgtgpy"urgekgu"cpf"uq o gvko gu"vjg { "ctg"tgi ctfgf"cu"eqpurgekŁeu0"Vjqug"yjq investigate hybridisation do not usually hold to a strict version of the biological species concept, accepting that successful mating between members of different species is commonplace. Wukpi"vjg"vqqu"qh"o qngewmct"i gpgvkeu."fgvgevki"i gpg"Ĥqy"jcu"dgeq o g"uvtcki jvhtyctf."dww" delimiting species boundaries can become even more problematic as we strive to distinguish retained ancestral polymorphisms from those that have introgressed and understand the long-vgt o "eqpugswgpegu"qh"nk o kvgf"i gpg"Ĥqy0"Vjgtg"ku"c"rgtegrvkqp"vjcv" |qqnqikuvu"jcxg"ceegrvgf" nguu"i gpg"Ĥqy"vjcp"dqvcpkuvu"y jgp"fguetkdkpi"fkuvkpev"urgekgu"\*dww"ugg"Tkuggdgti"gv"cn0"4228+0" Vjgtg"ctg."jqy gxtg."o cp{ "Pgy" \ gncn"p"gzco rngu"qh"tgeq i pkugf"cpko cn"urgekgu"vjcv"jcxg" nqy"ngxgnu"qh"i gpg"Ĥqy"ykvj"rctrcvtke"tgnvkvxgu."kpenwfkpi"rgtkrcvuu"\*Vtgykem"3; ; :="Vtgykem" 4222+."vtgg"y gvc"\*Oqti cp/Tkejctfu"3; ; 7="Vtgykem" ( "Oqti cp/Tkejctfu"3; ; 7+."dtqyp"vgcn" \*Dctvqp"4225+."rctcmggvu"\*Mgctxgn"gv"cn0"4225+"cpf"Łujgu"\*Guc"gv"cn0"4222+\*Hki 0"3+0" Cnvjqwi j" vjg"Pgy" \ gncn"p"Ĥqtc"jcu"dgpp"ekvgf"cu"jcxkpi"c"jki j"htgswgpe{ "qh"kpvturgekŁe"j { dtkfkucvkqp"

(III). Each section is further subdivided, but the physical location and consequences of hybridisation are discussed in detail in the text.

In particular, hybridisation of New Zealand species that in the recent (pre-human) past were geographically isolated has been well documented. Native species have come face to face with exotic species (Gillespie 1985; Gibbs 1987; Hitchmough et al. 1990) and range changes have occurred (Gillespie 1985; Gibbs 1987; Hitchmough et al. 1990). In particular, hybridisation of New Zealand species that in the recent (pre-human) past were geographically isolated has been well documented. Native species have come face to face with exotic species (Gillespie 1985; Gibbs 1987; Hitchmough et al. 1990) and range changes have occurred (Gillespie 1985; Gibbs 1987; Hitchmough et al. 1990).

*Pratia angulata* has hybridised with *Pratia acuta* (Gillespie 1985; Gibbs 1987; Hitchmough et al. 1990).

cdwpfcpeg\*gi0."uvkvu"\*OceCxq{ ("Ejco dgtu"3; ; ; = "I tggpg"3; ; ; + "cpf" rctcmggvu\*Ejcp"gv"cn0" 4228+ "cpf" etquu/hquvgtkpi "qh" dncem" tqdkpu" cpf" vq o vkvu\*Oc" ("Nc o dgtv"3; ; ; 9+0" Jw o cpu" ctg" cnuq" ko rnkcevfg" kp" vjg" nqy" pw o dgtu" qh" y gvc" qp" Dcpmu" Rgpkpuwnc\*Oqti cp/Tkejctfu" ("Vqy pugpf" 1995) and fur seals on Macquarie Island (Lancaster et al. 2006) where hybrids have been detected using genetic tools. In both these examples it is thought that relative abundance of species affects the selection of mates, increasing hybridisation when one species is relatively

tctg\* J wddu"3; ; 77+0" Nkmg y kug." hqt" cndcvtquu" qp" Ec o rdgnn" Kuncpf" kpvgt dtggf kpi "qh" v y q" qt" v j tgg" urgekgu" ku" gzcegt dcvfg" d{ "ncem" qh" eqpurgekL e" o cvgu" hqt" v j g" tctgt" dncem/ dtqy gf" hqt o" \*Oqqtg" et al. 2001).

" Hqtguv" engctpeg" qp" Ocpigtg" Kuncpf" kp" v j g" E j cvj c o" Kuncpfu" i tqwr" ku" v j qw i j v" vq" j cxg" r tq- o qvfg" qr rqt vwpkvkgu" hqt" j { dtkfkucvkqp" dgy y ggp" Hqtdguø" rctcmggvu" \*Cyanoramphus forbesi) cpf" E j cvj c o" Kuncpf" tgf/etqy pgf" rctcmggvu" \*C. novaezelandiae chathamensis+0" V j g" hqt o gt" species generally prefers forest habitats to open vegetation, while the latter generally resides

kp" qrgp" rcejgu" qh" i tcuu." uetwd" cpf" j gtdu" \*Vc{ nqt"3; ; 97+0" C" uwtxg{ "qh" o kvqej qpf tkcn" eqpvtqn" tgi kqp" FPC" ugs wgppeg" j crnqv{ rgu" fgvgvfg" i gpg" i qy" dgy y ggp" v j g" v y q" urgekgu" qh" rctcmggvu0" E j cvj c o" Kuncpf" tgf/etqy pgf" rctcmggv" o v FPC" j crnqv{ rgu" y gtg" kfgpvkL gf" kp" FPC" uc o ringu" qdvckpgf" htq o" Hqtdguø" rctcmggv" o qtr j qv{ rgu" \*Dqqp" gv" cn0" 4223= "Dcncpv{ pg" gv" cn0" 4226+0" Hwtv jgt" gzc o kpcvkqp" y kvj" o ketqucvgnkvg" o ctmgtu" j cu" u j q y p" v j cv" v j g" Ocpigtg" Kuncpf" Hqtdguø" rctcmggv" rqrwncvkqp" j cu" j { dtkfkugf" gzvgpukxgn{ "y kvj" E j cvj c o" Kuncpf" tgf/etqy pgf" rctcmggvu." vq" cp" gzvgpv" v j cv" v j g" t g" o c{ "pqv" gxgp" dg" c" ukp ing" vtwg" Hqtdguø" rctcmggv" y kvj qww" c" j kuvqt{ "qh" j { dtkfkucvkqp0" V j g" Ocpigtg" Kuncpf" rctcmggv" rqrwncvkqp" ku" pqy" eq o rqugf" rtg f q o kpcpv n{ "qh" et{ rvke" j { dtkfu" v j cv" tguggz o O

e r r \_ \$

j { dt" "v

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picornaviruses, coronaviruses, alphaviruses and retroviruses (Lai 1992). Retroviruses, in rctvkwnc."ctg"tgpqypgf"hqt"tgncvkggn{"tcrkf"tgeq"dkpcvkqp"tcvgu."qp"vjg"qtfgt"qh"4' "rgt"mknqdcug"rgt"tgrnkecvkqp"e{eng"Jw" ("Vg"okp"3; ;2+0" Tgvtqxkctn"tgeq"dkpcvkqp"qeewtu"kp"c"jquv" cell during reverse transcription when the infecting virion has a heterozygous genome (Hu ("Vg"okp"3; ;2+0 " Vjg"tgvtxktwu."HKX."c"enqug"tgncvkg"qh"JKX."jcu"dgpp"kf gpvkLgf"kp"fq"oguvke"ecvu"\**Felis catus*) in New Zealand (Swinney et al. 1989; Hayward et al. 2007). Phylogenetic tree construction of *envelope* (*env*+ "igpg"ugswgpegu"jcu"ujqyp"vjcv"vyq"qh"vjg"Łxg"rquukdng"HKX"uwdv{"rgu"ctg"hqwpf"kp" Pgy" \ gncpf" kphgevgf" ecvu" \* Jc{ yctf" gy" cn0" 4229+0" Vjgug"vyq"uwdv{"rgu."C"cpf" C, co-occur in cat populations, leading to dual infection and consequently recombination/ j{dtkf kucvkqp0" Cdqwv" 807' " \*n ?" 378+ "qh" Pgy" \ gncpf" HKX/ kphgevgf" ecvu" ctg" kphgevgf" ykvj" cp" A/C recombinant in the *env*" igpg" \* Jc{ yctf" ("Tqftki"q"422: +0" Vjgug"tgeq"dkpcpv"uvtkpu"ctg" circulating recombinant forms, that is, they are the viral progeny of the host cell where the recombination event occurred.

Viral recombination can repair substitution errors made by the enzyme reverse transcriptase, or can modify particular viral properties, such as virulence (Lai 1992). In this way, viruses are able to adapt to new environments, such as a new host species (Poss et al. 2007). Whatever the result of the crossover event, recombination is instrumental in the evolutionary history of viruses. In addition, viral recombination increases the genetic diversity of circulating viruses within a population, which has implications for vaccine use and development in New Zealand.

Cnvjqw i j" jcdkvcv" o qfkŁecvkqp" d{ " jw" ocpu" qhvpp" ngcfu" vq." qt" gzcegt" dcvgu" j{ dtkf kucvkqp." kv" ku" cp" important and common natural process too.

Genetically (and sometimes morphologically) distinct populations can meet and mate in spatio-vg" o rqtcm{"dqwpfgf"tg i kqpu"ecmgf"j{ dtkf" | qpgu" \* Jcttkuqp" 3; ; 5+0" Vjg" rqukvkqp" cpf" ykf vj" qh" c" zone is usually stable over many generations, due to equilibrium between the ability of organisms to disperse and the selective disadvantage suffered by the hybrid offspring (Barton & Jgykv" 3; ; 7+0" Hwtvjgt" uvcdknkv{ "ku" gpuwtf" y jgp" | qpgu" nkq" kp" fgpvk{ "vtqw i ju" \* Dctvqp" 3; 9; + "qt" on ecotones (Moore 1977). Most hybrid zones involve secondary contact of populations that jcxg" fkggti" gf" kp" kuqncvkqp0" Hqt" gzc" o r ng." c" urgekgu" Łqem" qh" i cnczkkf" Łujgu" \* *G. vulgaris sensu lato*) show some limited parapatric overlap in the South Island, as a result of natural secondary contact, and some of these contacts show occasional hybridisation (Allibone et al. 1996). Within the radiation of New Zealand cicadas many parapatric species form hybrid zones upon contact (Marshall et al. 2008). New Zealand tree weta hybrid zones have been described on mountain ranges (*Hemideina maori*, King et al. 1996, 2003) and in lowland forest (*H. thoracica*, Oqti cp/ Tkejctfu" gv" cn0" 4222- " Oqti cp/ Tkejctfu" (" Ycmku" 4225+0" Vjg" wug" qh" o wnvkrng" j{ dtkf" zones within the same species has allowed inferences about relative disadvantage suffered d{ " j{ dtkf" qhhurtkp i" ykvj" kp" gcej" | qpg0" Vjg" fku rgtucn" cdknkv{ "qh" *H. thoracica* individuals from different chromosome races is assumed to be identical and thus the difference in zone width is

Because the majority of hybrid zones form following secondary contact and taxa are often

destroyed forest in the central North Island and a number of independent genetic studies have

fern *Asplenium hookerianum* Shepherd et al. 2007). In addition, two chromosome races of the

(Morgan-Richards et al. 2000). Concordance of frequency clines for four other genetic loci

cause hybrid disadvantage. Chromosome heterozygotes often suffer reduced fertility compared

to chromosome homozygotes due to mal-segregation of chromosomes during gamete produc-

female tree weta may have lower dispersal rates compared to males, resulting in a narrow



**Historical gene flow (introgression)**

*Nothofagus* is a major component of forests throughout the South Island of New Zealand, and several hypotheses have been proposed to explain its absence across the central portion of the island. To distinguish between hypotheses, we found that through hybridisation, red beech (*Nothofagus fusca*) and hard beech (*N. truncata*) have absorbed genetic material from mountain beech (*N. solandri* var. *cliffortioides*). A single insertion in the *trnL-trnF* intergenic spacer is found within

introgression between *M. iolanthe* and members of the genus with similar songs, than lineage

### Contemporary gene flow

Despite considerable differences in morphology, *Pseudopanax lessonii* and *P. crassifolius* are genetically distinguishable as separate evolutionary lineages, and that the majority of their hybrids are uncommon, suggesting that *P. lessonii* and *P. crassifolius* only rarely cross directly and

When hybridisation results in a lineage reproductively isolated from its two parental taxa a pg y "ur gekgu"ku"cn o quv"kpucvpcpgqwun{"rtqfwegf0"fwg"vq"vjg"fkhlEwnv{"kp"tgrtqfwekpi"ykvjqwv"dcemetquukpi"vq"rctgpvcn"vczc."vjk"u"htq o"qh"ur gekcvkqp"ku"tctg"eq o rctgf"vq"vjg"tcvg"qh"j { dtkfkuc tion without speciation. However, it is possible for hybridisation to be followed by chromo- uq o g"fqwdnkp i"cpf"vjg"tguwnvki"kpfkxkfwcn"vq"tgrtqfweg"cuqzwcnn{"qt"d{"ugnLpi0"Gxkfgpeg"ht" fkrnqkf"j { dtkf"ur gekgu"htq o cvkqp"ku"y gcmgtl"U r gekcvkqp"xkc"j { dtkfkucvki"ku"o wej"nguu"eq o o qp" kp"cpk o cnu"vjcp"kp"rncpvu"dgecwug"kuqncvki" o ge jcpku o u"\*uwej"cu"ugnLpi+"ctg"nguu"nkmgn{"vq" evolve in concert with hybridisation. Chromosome doubling in animals can also have a dire effect on sex determination, and animals may be generally more susceptible to changes in gene dosage. *Pratia* discussed earlier is an example of new lineages arising from human induced range changes (Murray et al. 2004). In this case, hybrid lineages are recognised as distinct e j tq o quq o g"tcegu"\*pqv"pgy"ur gekgu+."dvv"ctg"vjg"tguwnv"qh"kpvtur gekL e"etquigu0"Dtgv y kgug" gv"cn0"3 ; ; ; + "wugf"gxkfgpeg"htq o"cf fkvxg"KVU"ugswgpegu"vq"uwr r rqtv"vjg"j { rqv j guku"vjcv"Ana- phalioides hookeri is a hybrid species with parentage *A. bellidioides* × *A. trinervis*. Since it has a tetraploid chromosome count ( $2n=4x=56$ ; Groves 1977), it is presumably an example of allopolyploidy (hybridisation followed by chromosome doubling to produce an independent hybrid lineage). In New Zealand buttercups, *Ranunculus nivicola* is an allopolyploid species with *R. verticillatus* and *R. insignis*"rctgpvu0"V jg"fg i tgg"qh'er FPC"u jctkpi"dgvy ggp"R. insignis and *R. enysii* suggest that these two species have also been hybridising and *R. insignis* may even be of hybrid origin itself (Carter 2006).

" Rqn{rnqkf{"ku"ceq o o qp"r jgpq o gpqp"co qpi uv"Pg y "\ gncpfa"hgtpu0"cn"ur gekgu"qh"Asple- nium native to New Zealand are at least tetraploid and, of the 17 species in the Austral group, nine are octoploid. cpDNA and nuDNA (*Leafy*) indicate that most of these octoploids are allopolyploids (Perrie & Brownsey 2005a; Shepherd et al. 2008a). cpDNA of the octoploids is very similar to their parental species, suggesting recent origins with little time to develop autapomorphies (Shepherd et al. 2008b). In some cases, octoploids share multiple chloroplast types with each other and their progenitors, indicating repeated polyploidisation events (*A. gracillimum*, *A. cimmeriorum* (Perrie & Brownsey 2005b)). Allopolyploidy in New Zealand ferns has also been documented using molecular approaches in *Polystichum*, where *P. neoze- landicum* is an allo-octoploid of the tetraploids *P. wawranum* and *P. oculatum* (Perrie et al. 2003). Chloroplast sequences indicate that the tetraploid *Hypolepis ambigua* may be composed qh"kp fgrgp fgpvn{"fgtkxgf"cnmqrn{rnqkf"nkpgc i gu"qh"wpmpqy p"rctgpvc i g"\*Rgttkg" ("Dtqy pug{" unpubl.), whereas morphological comparisons suggest that the tetraploid *Pteris macilenta* is almost certainly an allopolyploid derivative of *P. comans* and *P. saxatilis* (Braggins 1975).

" Cnwjqwi j { dtkf

Alternatively, there may have been three (rather than two) sexual species involved in the multiple hybridisation and many origins creating the current diversity.

Łvpguu"cpf"cfcrvcvkqpu."cpf"rtqxfkgu"tcy"fcvc"hqt"cpn{uku"qh"igpgu"kpqxngf"kp"rqv|{iqvke"kuqncvkqp"kp"j{dtkfu."uq/ecmgf"ōurgekvkqp"igpgu"Qt"gv"cn0"4226+0"Hqt"gzco ring."vjg"pgy" generation of sequencing technology will allow the biochemical pathway and alleles respon- ukdng"hqt"icogvg"\*rqmngp."urgt o+"eqo rgvkvkqp"vq"dg"kfgpvkŁgf"cpf"vjwu"vjgkt"tqng"kp"nk o kvkpi" j {dtkfkucvkqp"y knn"dg"wpfgtuvqqf0"Vtcpuetrvg o g"cpn{uku"vj tqw i j "kuqncvkqp"qh" o TPCu"cnuq" allows estimation of gene expression, touted by many to be at least as important as structural changes to the genes in question (King & Wilson 1975). It could be, for example, that hybrid dtgcmfqy p"ku"cvtkdwdcdng"vq"ejcpigu"kp"igpg"gzrtguukqp"ecwugf"d{ "pqxgn"kpvgtcevkqpu"dgvy ggp" vyq"vtpuetkrvkqpcn"pgvy qtmu"\*Ncpft {"gv"cn0"4229+0

In cases such as *Phormium* and *Pseudopanax* ecological selection may be critically important in maintaining species differences in the face of extensive hybridism and an apparent absence qh"tqdwuv"kpvtkpuke"dcttkgtu"vq"igpg"Łqy0"Kp"qvjgt"itqwru."uwej"cu"vjg"Raoulia alliance, genetic divergence between hybridising species appears to be greater, and intrinsic barriers to gene Łqy"ctg"itgcvgt."dvw"ugngcvkqp"ci ckpuv"tgeq o dkpcpv"igpqv{ rgu"ku"uvknn"nkmg n {"vq"dg"ko rqtvcpv"kp" nk o kvkpi"igpg"Łqy0"Kp"eqpvtcuv."vtgg"y gvc"j cxg"tgncvkggn {"jki j "ngxgnu"qh"igpgvke"fkxgtukv {"vjcv" fcvg"vq"igqi tcrjke"kuqncvkqp"fwtkpi"vjg"Rnkqegpg." {gv"rqrwncvkqpu"ykvj"fkuvkpev"mct {qv{rgu" failed to speciate, possibly due to simple mate recognition systems in this genus.

" Vjg"tqng"qh"j {dtkfkucvkqp"kp"kpxcukqp."tcpig"gzrcpukqp"cpf"cfcrvcvkqp"vq"enk o cvg"ejcpigu" ku"cpqvjgt"mg {"ctgc"nkmg n {"vq"rtqxfkg"uvk o wncvkpi"tgugetej0"Vjg"gxqnwvkqp"qh"kpxcukxgpguu"ku" hceknkvcvgf"d {"j {dtkfkucvkqp"cpf"vjg"tgncvkqpujkr"dgvy ggp"ci g"qh" Pgy" \gcncpfø"dkqvc"cpf" rtqrqtvkqp"qh"j {dtkf"urgekgu"eqwnf"urctm"eq o rctcvkxg"uvvfkgu"qh"dqvj"kuncpf"cpf"eqpvkpgpvcn" ecosystems. One might view hybrid species as evidence of recent dispersal or invasion, but uvwf {"qh"vjg"igpgvkeu"qh"yggf{/pguu"cpf"vjg"j {dtkf"igpq o g"y knn"dg"o qtg"rtqfwevkg0"Htq o "qwt" understanding of the history and processes that have shaped the distribution and abundance of ewttgpv"vczc"yg"ecp"o cmg"rtgfkewkqpu"qh"jqy"qwt"Łqtc"cpf"hcwpc"y knn"tgurqp"vq"vjg"ewttgpv"

\*5+ "Vjg"ko rqtvcv"tqng"qh"j { dtkfkucvkqp"kp"vjg"gxqmwkqp"qh"Pyg "\ gcncpfø"gpfg oke"rncpvu"cpf" animals has been highlighted by recent genetic studies. Recent hybrid origins of ferns, dwwgtewru."gxgtncuikp i "fckukgu"cpf"uvkem"kpugevu"kpfkcev"vjg"qp i qkp i "i gpgtcvkqp"qh"dkqfk-

Bordewich M, Semple C 2007. Computing the minimum number of hybridization events for a consistent evolutionary history. *Discrete Applied Mathematics* 155: 914–928.

Dtc i ikpu LG3 ;970Uvwfkgu qp v jg Pgy \ gncp f .cp f uq o g tgcvgf .ur geku qh Pteris

Hgttku"UF."Uci"TF." Jwcp"E/O." Pkgnugp"LV."Tkwyg"W." Yknuqp"CE"3; :50"Hnqy"qh" o kvqejqpfkcn" FPC"  
across a species boundary. Proceedings of the National Academy of Sciences USA 80: 2290–2294.  
Hkv|rcvtkem"DO."Ujchgt" JD"42290" J {dtkf" xkiqt" dgyyggp"pcvkg"cpf"kpvtqfwegf"ucnc ocpfgtu" tckugu"  
new challenges for conservation. Proceedings of the National Academy of Sciences USA 104:  
15793–15798.







Uokuugp"TF."Dtgvkykgugt"K."Yctf"LO."OeNgpcejcp"RC."Nqemjctv"RL"42250"Wug"qh"KUUT"rtqLngu"cpf"  
KVU/ugswgpegu"vq"uwvf{"vjg"dkqigqitcrj{"qh"cnrkpg"ewujkqp"rncpvu"kp"vjg"igpwu"*Raoulia* (Asteraceae).  
Plant Systematics and Evolution 239: 79–94.

Uokuugp"TF."Dtgvkykgugt"K."Yctf"LO"42260"Rj{"nqigpgvke"ko rnkecvkqpu"qh"vtcpu/urgekLe"ejnqtqrncuv"  
DNA sequence polymorphism in New Zealand Gnaphalieae (Asteraceae). Plant Systematics and  
Evolution 249: 37–53.

Uokuugp"TF."Jggpcp"RD"42290"FPCLpigtrtkpki"uwrrqtvu"j{dtkfk{ovkqp"ou"c Ooq\$ o qpipi"u\$

- Ygdd"EL."U{mgu"YT."Ictpqem/Lppgu"RL"3;::0"Hnqtc"qh"Pgy"\gcncpf<"pcwvtnkugf"rvgtkfqrj{vgu."gymnosperms, dicotyledons. Botany Division, DSIR, Christchurch, New Zealand.
- Ykej ocp"UT."Ytkijv"UF."Ecogtqp"GM."Mggnkpi"FL."Ictfpgt"TE"42240"Gngxcvgf"igpgvke"jgvtqi gpgkv{"and Pleistocene climatic instability: inferences from nrDNA in New Zealand *Coprosma* (Rubiaceae). *Lqwtpcn*"qh"Dkqigqitcrj{"4;<";656;760
- Yknvqp"CF."Dtgvkykgugt"K"42220"Eqorqukvkqp"qh"vjg"Pgy"\gcncpf"uggf"rncpv"lqtcl"Pgy"\gcncpf"Lqwtpcn"of Botany 38: 537–549.
- Ykpm y qtvj"TE."Dt{cp" F."Nqemjctv"RL."Jcxgmn" F."Oqwnvqp"X"42270"Dkqigqitcrjke"kpvgtrtgvckvqp"qh"splits graphs: least squares optimization of branch lengths. *Systematic Biology* 54: 56–65.