

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. This hybridisation is highlighted.

"*Equus caballus* × *Equus asinus* hybridisation in New Zealand: a review of the literature and a new record from the North Island." *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. In New Zealand, hybridisation can create new species (Kraus & Miyamoto 1990;

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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" ("Pqqt"4225+."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"igpgvke"vqqnu."Pgy"\gcncpf"dknqiku"jcxg"vcmgp"vjg"qrrqtvwpkv{" to investigate old hypotheses and erect new ones concerning hybridisation. Multilocus monogenic o ctmgtu"rgt o kv"fgvgevkqp"qh"dqj"qp i qkp i"cpf"jkuvqtkecn"i gpg"i qy"c o qp i"nkpgc i gu"cpf" 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 qh"i qqf"vk o g"mgg rkp i"htq"eqpuvtckp i"vjg"ci g"qh"Etuv"eqpvev"htq" o cp {" j { dtkfkukp i"vczc"Vjg" 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 wu"k o rcev"kp"vjg"kpvtgpcvkqpcn"uekgpvkE"eq o o wpkv {"*htq"gzc o rng"J wuqp"4227="Ykpm y qtvj"gv" cnl"4227="Dctqpk"gv"cnl"4228="OeDtgpp" ("Nqemjctv"4228="Dqtfgykej" ("Ug o rng"4229="Lqn {"gv" al. 2007, in press a; Holland et al. 2008).

Hybridisation has been at the centre of three debates in evolutionary biology: species concept. "urgekcu"eqpugtvcvkqp."cpf"qtki kp"qh"pgy" i qtc"cpf"hcwpc"kp"gcej"qh"vjgug"vjgg"ctgcu." New Zealand studies offer new information or a different perspective.

Vjg"kf gpvkEcvkqp"cpf"fgLpvkqp"qh"urgekcu"qhvgp"tghgtu"vq"vjg"cdknkv {"qh"kp f kxfwcnu"htq o" Fkhgtgpv"qrrwncvkpu"vq" o cvg"cpf"rtqfweg"cv"hgcu"uq o g"hgtkng"qhhu rtkp i"Vjg"dknq i kecn"urgekcu" concept (Mayr 1942) is based on the principle that different species do not exchange genes,

J { dtkfkucvkqp"ku" c" eq o o qp"cpf"ko rqtvcpv"gxqnvkqpc {"rtqeguu"yqtnfykfg"Vjg"nqpi/vgt o" qwveq o g"qh"j { dtkfkucvkqp"ku"fg r gpf gpv"qp"vjg"tgncvkg"Lyvguu"qh"vjg"j { dtkfu"cpf"uudgswgpp"i gpgtcvkqpu." compared to the parental taxa, as illustrated by the following New Zealand examples.

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

uq"kf gpvkLecvkqp"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"eqpurgekLēu0"Vjqug"y j q" 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"vqqnu"qh" o qngewmct" i gpgvkeu." fgvgvki" i gpg" ĩ qy" jcu" dgeq o g"uvtcki jvhtyctf." dwv" 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" ĩ qy0"Vjgtg"ku"c" rgtgrvkqp"vjcv" |qqnqikuvu"jcxg"ceegrvgf" nguu" i gpg" ĩ qy" vjcp"dqvcpkuvu"y jgp"fguetkdkpi"fkuvkpev"urgekgu"*dwv"ugg"Tkuggdgti"gv"cn0"4228+0" Vjgtg"ctg." j qy gxtg." ocp{ "Pgy" \ gncp" gzc o rngu"qh" tgeq i pkugf" cpk o cn"urgekgu"vjcv" jcxg" nqy"ngxgnu"qh" i gpg" ĩ qy" ykvj" rctrcvtke"tgncvkgu."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"*Mgetxgn"gv"cn0"4225+"cpf"Łujgu"*Guc"gv"cn0"4222+*Hki 0"3+0" Cnvj qwi j" vjg"Pgy" \ gncp" ĩ qtc"jcu"dgpp"ekvgf"cu"jcxkpi" c"jki j"htgswgpe{ "qh"kpvturgekLē"j { dtkfkucvkqp"

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

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* (Gibbs 1987; Hitchmough et al. 1990).

cdwpcpeg*gi0."uvkvu"*OceCqx{ ("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" pwo 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" vj tgg" urgekgu" ku" gzcegt dcvfg" d{ "ncem" qh" eqpur gekLe" o cvgu" hqt" vj g" tctgt" dncem/ dtqy gf" hqt o " *Oqqtg" et al. 2001).

" Hqtguv" engctpeg" qp" Ocpigtg" Kuncpf" kp" vj g" Ejcvjc o "Kuncpfu" i tqwr" ku" vj qwi j v" vq" j cxg" rtq- o qvgf" qrrqt vwpkvkgu" hqt" j { dtkfkucvkqp" dgy y ggp" Hqtdguø" rctcmggvu " *Cyanoramphus forbesi" cpf" Ejcvjc o "Kuncpf" tgf/etqy pgf" rctcmggvu " *C. novaezelandiae chathamensis+0" Vjg" 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 wpgpeg" j crnqv { rgu" fgvgvfg" i gpg" i qy " dgy y ggp" vj g" v y q" urgekgu" qh" rctcmggvu" 0" Ejcvjc o "Kuncpf" tgf/etqy pgf" rctcmggvu" o vFPC" j crnqv { rgu" y gtg" kfgpvkLgf" kp" FPC" uc o ringu" qdvckpgf" htq o "Hqtdguø" rctcmggvu" o qtr j qv { rgu" *Dqqp" gv" cn0" 4223= "Dcncpv { pg" gv" cn0" 4226+0" Hwtvjgt" gzc o kpcvkqp" y kvj " o ketqucvgnkvg" o ctmgtu" j cu" ujqyp" vj cv" vj g" Ocpigtg" Kuncpf" Hqtdguø" rctcmggvu" rqrwncvkqp" j cu" j { dtkfkugf" gzvgpukxgn { " y kvj " Ejcvjc o "Kuncpf" tgf/etqy pgf" rctcmggvu." vq" cp" gzvgpv" vj cv" vj g" tgu" o c { "pqv" gxgp" dg" c" ukping" vtwg" Hqtdguø" rctcmggvu" y kvj qww" c" j kuvqt { "qh" j { dtkfkucvkqp" 0" Vjg" Ocpigtg" Kuncpf" rctcmggvu" rqrwncvkqp" ku" pqy" eq o rqugf" rtg fq o kpcpvn { "qh" et { rvke" j { dtkfu" vj cv" tguggz o O

e r r _ \$

j { dt" "v

j { dt" w" qptekcp qntkndqrwncvk { "

picornaviruses, coronaviruses, alphaviruses and retroviruses (Lai 1992). Retroviruses, in rctvkewnc."ctg"tgpqypgf"hqt"tgnvckxgn{"tcrkf"tgeq odkpcvkqp"tcvgu."qp"vjg"qtfgt"qh"4' "rgt"mknqdcug"rgt"tgrnkcevkqp"e{eng"Jw" ("Vg okp"3; ;2+0" Tgvtqxkctn"tgeq odkpcvkqp"qeewtu"kp"c"jqv" cell during reverse transcription when the infecting virion has a heterozygous genome (Hu ("Vg okp"3; ;2+0

" Vjg"tgvtxktwu."HKX."c"enqug"tgnvckxg"qh"JKX."jcu"dgpp"kf gpvkŁgf"kp"fq o guvke"ecvu"**Felis catus*) in New Zealand (Swinney et al. 1989; Hayward et al. 2007). Phylogenetic tree construction of *envelope* (*env*+ "i gpg"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 {dtfkucvkqp0" Cdqwv"807' '*n ?"378+"qh" Pgy" \ gncpf" HKX/kphgevgf"ecvu"ctg" kphgevgf"ykvj"cp" A/C recombinant in the *env*"i gpg"* Jc{yctf" ("Tqftki q"422: +0"Vjgug"tgeq odkpcv"uvtckpu"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 o cpu"qhvgp"ngcfu"vq."qt"gzcegtdcvgu"j {dtfkucvkqp."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 ikpu"ecmgf"j {dtkf" | qpgu"* Jcttkuqp"3; ;5+0"Vjg"rqukvkqp"cpf"y kfvj"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 & Jgykvv"3; ;7+0" Hwtvjgt"uvcdknkv{"ku"gpwgtf"y jgp" | qpgu"nkg"kp"fgpvk{"vtqw i ju"*Dctvqp"3; ;9;+"qt" on ecotones (Moore 1977). Most hybrid zones involve secondary contact of populations that jcxg"fkxgti gf"kp"kuqncvkqp0" Hqt"gzc o rng."c"urgekgu"Łqem"qh"icnczkkf"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"qhhrtkp i" ykvj kp" gcej" | qpg0"Vjg"fkurgtucn"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 been conducted (e.g. *Xqne* *cevk* *cv* *vjg* *Ncmg* *Vewrq* *ecnf* *gtc* *jcu* *tgrg* *cvgn* *hqw* *pf* *vjcv* *fku* *kpev* *rqr* *wncv* *kqpu* *o* *ggv* *pgct* *Ncmg* *Vewrq* **g* *o* *i* *o* *u* *j* *q* *t* *v* *v* *c* *k* *n* *g* *f* *d* *c* *v* *N* *n* *q* *{* *f* *"* *4* *2* *2* *5* *=* *"* *ecd* *bage* *tree*, *Armstrong* *unpubl.*; the parasitic plant *Dactylanthus taylorii* *Holz* *zapfel* *et* *al.* 2002; fern *Asplenium hookerianum* *Shepherd* *et* *al.* 2007). In addition, two chromosome races of the *Cwemncpf* *vtgg* *y* *gvc* **Hemideina thoracica* *o* *ggv* *cpf* *kp* *v* *g* *t* *d* *t* *g* *g* *f* *q* *p* *v* *j* *g* *u* *j* *q* *t* *g* *q* *h* *"* *Ncmg* *Vewrq* (Morgan-Richards *et* *al.* 2000). Concordance of frequency clines for four other genetic loci **y* *q* *c* *nnq* *|* *{* *o* *g* *"* *q* *p* *g* *o* *ket* *q* *u* *c* *v* *g* *m* *k* *v* *g* *n* *q* *e* *w* *u* *."* *o* *v* *F* *P* *C* *+* *e* *q* *p* *L* *t* *o* *u* *"* *v* *j* *cv* *v* *j* *ku* *"* *c* *"* *u* *g* *e* *q* *p* *f* *ct* *{* *"* *e* *q* *p* *v* *ce* *v* *|* *q* *p* *g* *"* *d* *g* *v* *y* *g* *g* *p* *"* *v* *y* *q* *"* *t* *c* *e* *g* *u* *"* *q* *h* *"* *v* *t* *g* *g* *"* *y* *g* *v* *c* *"* *V* *j* *g* *"* *y* *k* *f* *v* *j* *"* *cp* *f* *"* *e* *g* *p* *v* *t* *g* *u* *"* *q* *h* *"* *v* *j* *g* *"* *h* *t* *g* *s* *w* *g* *p* *e* *{* *"* *e* *n* *k* *p* *g* *u* *"* *q* *h* *"* *c* *nn* *"* *L* *x* *g* *"* *n* *q* *e* *k* *"* *x* *ct* *{* *"* *x* *g* *t* *{* *"* *n* *k* *v* *v* *n* *g* *"* *V* *j* *g* *"* *p* *c* *t* *t* *q* *y* *g* *u* *v* *"* *q* *h* *"* *v* *j* *g* *"* *h* *t* *g* *s* *w* *g* *p* *e* *{* *"* *e* *n* *k* *p* *g* *u* *"* *ku* *"* *h* *q* *t* *"* *v* *j* *g* *"* *e* *j* *t* *q* *o* *q* *u* *q* *o* *g* *"* *t* *g* *c* *t* *t* *c* *p* *i* *g* *o* *g* *p* *v* *"* *V* *j* *ku* *"* *t* *g* *c* *t* *t* *c* *p* *i* *g* *o* *g* *p* *v* *"* *ku* *"* *g* *k* *v* *j* *g* *"* *v* *j* *g* *"* *f* *k* *t* *g* *e* *v* *"* *ec* *w* *u* *g* *"* *q* *h* *"* *j* *{* *d* *t* *k* *f* *"* *f* *k* *u* *c* *f* *x* *c* *p* *v* *c* *i* *g* *."* *q* *t* *"* *ku* *"* *n* *k* *p* *m* *g* *f* *"* *v* *q* *"* *n* *q* *e* *k* *"* *v* *j* *cv* *"* *cause* *hybrid* *disadvantage*. *Chromosome* *heterozygotes* *often* *suffer* *reduced* *fertility* *compared* *to* *chromosome* *homozygotes* *due* *to* *mal-segregation* *of* *chromosomes* *during* *gamete* *production* **o* *g* *k* *q* *u* *ku* *"* *V* *j* *g* *"* *p* *c* *t* *t* *q* *y* *g* *u* *v* *"* *q* *h* *"* *v* *j* *g* *"* *q* *v* *j* *g* *"* *h* *q* *w* *"* *h* *t* *g* *s* *w* *g* *p* *e* *{* *"* *e* *n* *k* *p* *g* *u* *"* *u* *g* *g* *p* *"* *kp* *"* *v* *j* *g* *"* *y* *g* *v* *c* *"* *cv* *"* *V* *ew* *r* *q* *"* *ku* *"* *h* *q* *t* *o* *g* *f* *"* *d* *{* *"* *v* *j* *g* *"* *o* *v* *F* *P* *C* *=* *"* *kp* *"* *e* *q* *p* *v* *t* *c* *u* *v* *"* *v* *q* *"* *v* *j* *g* *"* *e* *j* *t* *q* *o* *q* *u* *q* *o* *g* *u* *."* *ku* *"* *w* *p* *n* *k* *m* *g* *n* *{* *"* *v* *j* *cv* *"* *v* *j* *g* *"* *o* *kv* *q* *e* *j* *q* *p* *f* *t* *k* *cn* *"* *i* *g* *p* *q* *o* *g* *"* *ku* *"* *n* *k* *p* *m* *g* *f* *"* *v* *q* *"* *n* *q* *e* *k* *"* *w* *p* *f* *g* *t* *"* *u* *g* *n* *g* *e* *v* *k* *q* *p* *"* *J* *q* *y* *g* *x* *g* *t* *."* *o* *v* *F* *P* *C* *"* *ku* *"* *q* *p* *n* *{* *"* *o* *cv* *g* *t* *p* *c* *m* *n* *{* *"* *kp* *j* *g* *t* *k* *v* *g* *f* *"* *cp* *f* *"* *female* *tree* *weta* *may* *have* *lower* *dispersal* *rates* *compared* *to* *males*, *resulting* *in* *a* *narrow* *o* *v* *F* *P* *C* *"* *e* *n* *k* *p* *g* *"* *t* *g* *n* *c* *v* *k* *x* *g* *"* *v* *q* *"* *v* *j* *g* *"* *e* *n* *k* *p* *g* *w* *t* *cn* *"* *p* *w* *e* *n* *g* *c* *t* *"* *n* *q* *e* *k* *"* *u* *g* *g* *p* *"* *cv* *"* *V* *ew* *r* *q* *"*

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"kpucpvcpgqwun{"rtqfwegf0"fwg"vq"vjg"fkhlEwnv{"kp"tgrtqfwekpi"ykvjqwv"dcemetquukpi"vq"rctgpvcn"vczc."vjku"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"fqwdnkpi"cpf"vjg"tguwnvki"kpfkxfwcn"vq"tgrtqfweg"cuqzwcnn{"qt"d{"ugnLpi0"Gxkfgpeg"ht" fkrnqkf"j { dtkf"ur gekgu"htq o cvkqp"ku"y gcmgt0"U r gekcvkqp"xkc"j { dtkfkucvki"ku"o wej"nguu"eq o o qp" kp"cpk o cnu"vjcp"kp"rncpvu"dgecwug"kuqncvki" o gejcpi"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"etquigul"Dtgkvykgug" gv"cn0"3 ; ; ; +"wugf"gxkfgpeg"htq o "cf fkvxg"KVU"ugswgpegu"vq"uwr r qtv"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"ujctki"dgvyggp"*R. insignis* and *R. ensyii* 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 gpp"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. cimteriorum* (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 fgrgpfgpvm{"fgtkxgf"cnmqrqn{rnqkf"nkpgci"gu"qh"wpmpqyp"rctgpvcig"*Rgttkg" ("Dtqypug{" unpubl.), whereas morphological comparisons suggest that the tetraploid *Pteris macilenta* is almost certainly an allopolyploid derivative of *P. comans* and *P. saxatilis* (Braggins 1975).

" Cnvjqwi"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"cfrcvkvkqpu."cpf"rtqxfkgu"tcy"fcvc"hqt"cpn{uku"qh"igpgu"kpqxngf"kp"rqv|{iqvke"kuqncvkqp"kp"j{dtkfu."uq/ecmgf"đurgekvkqp"igpguö"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."urgto+"eqorgvkvkqp"vq"dg"kfgpvkŁgf"cpf"vjwu"vjgkt"tqng"kp"nko kvkpi" j{dtkfkucvkqp"yknn"dg"wpfgtuvqqf0"Vtcpuetrvqog"cpn{uku"vj"tqw"ij"kuqncvkqp"qh"oTPCu"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 dtgcmfqyp"ku"cvtkdwcdng"vq"ejcpigu"kp"igpg"gzrtguukqp"ecwugf"d{"pqxgn"kvptcevkqpu"dgvyggp" vyq"vtcpuetrkvkqpcn"pgvyqtmu"*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"tdwuw"kpvtkpuke"dcttkgtu"vq"igpg"Łqy0"Kp"qvjgt"itqwrū."uwej"cu"vjg"Raoulia alliance, genetic divergence between hybridising species appears to be greater, and intrinsic barriers to gene Łqy"ctg"itgcvgt."dwv"ugngcvkqp"ci ckpuv"tgeqodkpcpv"igpqv{rgu"ku"uvknn"nkmg"{"vq"dg"ko rqtvcpv"kp" nko kvkpi"igpg"Łqy0"Kp"eqpvtcuv."vtgg"ygv"jcxg"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"kpvcukqp."tcpig"gzrcpukqp"cpf"cfrcvkvkqp"vq"enkocvg"ejcpigu" ku"cpqvjgt"mg{"ctgc"nkmg"{"vq"rtqxfkg"uvkwncvki"tgugetej0"Vjg"gxqnvkqp"qh"kpvcukxgpguu"ku" heeknkvcvgf"d{"j{dtkfkucvkqp"cpf"vjg"tgncvkqpujkr"dgvyggp"ci g"qh" Pgy" \gcncpf0"dkvc"cpf" rtqrqtvkqp"qh"j{dtkf"urgekgu"eqwnf"urctm"eqo rctcvkxg"uvfkgu"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"igpqog"yknn"dg"oqtg"rtqfwevkxg0"Htqo"qwt" understanding of the history and processes that have shaped the distribution and abundance of ewttgpv"vczc"yg"ecp"ocmg"rtgfkvkvkqpu"qh"jqy"qwt"Łqtc"cpf"hcwpc"yknn"tgurqp"vq"vjg"ewttgpv"

*5+ "Vjg"ko rqtvcv"tqng"qh"j { dtkfkucvkqp"kp"vjg"gxqmwkqp"qh"Pyg "\ gcicpfø"gpfg oke"rncpvu"cpf" animals has been highlighted by recent genetic studies. Recent hybrid origins of ferns, dwwgtewru."gxgtncuikpi" 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;970"Uvwfkgu"qp"vjg"Pg y"\ gncp f."cp f"uq o g"tgncv g f."ur geku"qh"*Pteris*

Hgttku"UF."Uci g"TF." J wcp"E/O." Pkgnugp"LV."Tkwyg"W." Yknuqp"CE"3; :50"Hnqy"qh" o kvqejqpftkn"FPC"
across a species boundary. Proceedings of the National Academy of Sciences USA 80: 2290–2294.
Hkv|rcvtkem"DO."Ujchhgt" JD"42290" J {dtkf" xki qt" dgyyggp"pcvixg"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"uvwf{"vjg"dkqigqitcrj{"qh"cnrkpg"ewujkq"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{ovkq"ou"c Ooq\$ o qpipi"u\$

- Ygdd"EL."U{mgu"YT."Ictpqem/Lppgu"RL"3;::0"Hnqtc"qh"Pggy"\gcncpf<"pcwvtnkugf"rvgtkfqrj{vgu."gymnosperms, dicotyledons. Botany Division, DSIR, Christchurch, New Zealand.
- Ykej ocp"UT."Ytkijv"UF."Eco gtqp"GM."Mggnkpi"FL."Ictfpgt"TE"42240"Gngxcvfgf"igpgvke"jgvgtqi gpgkv{"and Pleistocene climatic instability: inferences from nrDNA in New Zealand *Coprosma* (Rubiaceae). *Lqwtpcn"qh"Dkqigqitcrj{"4;<"656;760*
- Yknvqp"CF."Dtgv ykgugt"K"42220"Eqo rqukvkqp"qh"vjg"Pggy"\gcncpf"uggf"rncpv"l qtc0"Pggy"\gcncpf"Lqwtpcn"of Botany 38: 537–549.
- Ykpm yqtvj"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.